Guild structure of the large marsupial carnivores in Tasmania

by

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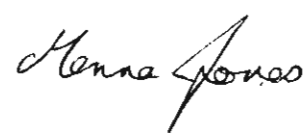

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Abstract

The principal focus of community ecology is to detect patterns in natural assemblages of plants and animals and explain the causal factors that underlie them. For the last 30 years, much of ecological theory has assumed that competition is the primary structuring force in communities. Competition is likely to be most important at the lower levels of community organisation, that of the guild. At the scale of large geographic regions, both evolutionary history and the physical environment are important in determining the composition of species assemblages. The structure of the guild of large dasyuroids or marsupial carnivores in Tasmania, Australia, is examined in relation to causal factors, especially the importance of competition. The relative significance of evolutionary history and the physical environment in shaping the composition of the Australian marsupial carnivore fauna is assessed.

Evidence that competition was and still is an important structuring force in the guild is found. Evolutionary evidence is found in character displacement and morphological size patterning in canine strength, the trophic structure proximally related to feeding ecology of the large dasyuroids. The hypothesis of competition as the underlying causal factor is supported by similar patterning in prey size and a carnivore body size / prey size correlation. The existence of current competition in the guild can be inferred from the large extent of dietary overlap between species. The effects of competition are most evident between the two most similar species, the congeneric quolls. Resources are partitioned on at least three niche dimensions, diet, horizontal and vertical use of the habitat. Where dietary overlap is high between species, habitat use overlap is low, thereby reducing the potential for direct competition for individual prey items. Interference competition is most likely to occur over large carcasses. Mainly body size but also age of the carnivore determine interspecific dominance. Devils are usually dominant and are the primary scavengers, exhibiting adaptations for scavenging that are lacking in the other two species.

Aspects of guild structure are influenced by several factors as follows. Size relationships in both body size and trophic structures are influenced by - latitudinal size correlations, competitive character displacement, size distributions of prey species which are shaped by the fractal dimensions of the habitat, and sexual selection. Locomotor morphology and habitat use of the carnivore species show evolutionary adaptations that match the arboreal or terrestrial habits of their particular size range of prey species. Competition may result in the depression of species populations. The rarity of spotted-tailed quolls can possibly be explained by higher dietary overlap and competition than is experienced by the other species. Numerical dominance of the guild by devils may relate in part to large body size and behavioural dominance in feeding situations.

Substantial ecological convergence has occurred between the marsupial carnivore fauna of Australia and eutherian carnivore faunas on other continents. The main differences are the low diversity of species and eco-morphological types in Australia, which relate to poor soils and aridity. This supports the general view that the physical environment is more important than evolutionary history in shaping the composition of faunal assemblages.

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Guild /gild/, *n.* **1.** an organisation of persons with common professional or cultural interests formed for mutual aid and protection. **2.** one of the associations, numerous in the Middle Ages, formed for mutual aid and protection or for a common purpose, most frequently by persons associated in trade or industry.

(The Macquarie Dictionary, Macquarie University, Sydney, 1991)

The emphasis on competitive interactions and predation as major structuring forces in ecological communities and the deemphasis of mutualism may reflect a social background and world view as much as the nature of nature. This is the same world view that considers unfettered capitalism to be "natural", with self-regulatory traits analogous to those of a supposed "balance of nature". (Simberloff and Dayan, 1991, citing Boucher, 1985; Leigh, 1971 and Risch and Boucher, 1976)

Chapter 1 General Introduction

1.1 Background and Aims

The principal focus of community ecology is to detect patterns in natural assemblages of plants and animals and explain the causal factors that underlie them. A central debate over the last twenty-five years has been the importance of the various mechanisms of ecological interactions in structuring communities. These mechanisms are either: interactions between species, including competition, predation, mutualism, parasitism and disease; or physical environmental forces such as low nutrients, spatial and temporal heterogeneity and stochastic perturbation events like floods and droughts. Competition has been thought to be of overriding importance, although more recently, researchers have explored the roles of non-equilibrium, stochastic events, parasitism and disease (MacArthur, 1972; Cody, 1975; Diamond & Case, 1986; Dobson & Hudson, 1986). The view that competition has a central role in structuring communities was formalised in 1934 by Gause in his 'Competitive Exclusion Principle'. This states that similar, competing species coexist by niche differentiation (den Boer, 1986). As a result of Gause's studies, the emphasis in biology shifted from evolutionary issues of the origin of diversity to ecological issues involving the 'maintenance of diversity' or how species coexist (Schoener, 1986).

The prevalence of competition in natural communities is one of the fundamental questions in community ecology. Answering this question is fraught with difficulties. Other forces that influence community structure may depress populations below the density at which competition becomes an issue. In some situations competition may be intense but patchiness of the environment enables species to coexist. Competition may have been an important structuring force in an assemblage of species but has resulted in morphological coevolutionary change. The result of this is to reduce competition. Therefore, current competition cannot be demonstrated. Connell (1980) called this the "ghost of competition past" (Begon, Harper & Townsend, 1990)

It is possible to demonstrate active depressive competition between species by controlled experiments where densities of each species are manipulated. Natural communities, however, are so complex that unambiguous experiments can be difficult to execute. Ecologists have looked instead for patterns in species distributions, morphological size relationships and differential resource use, or resource partitioning, that suggests the existence of competition as the underlying causal factor. A rigorous approach of hypothesis falsification and null models was brought to science in the late 1970s and early 1980s with the application of the philosophies of Karl Popper. Despite the problems of ensuring that the null models are themselves truly null and free of the effects of competition, this approach has enabled the evaluation of perceived patterns as to whether the observed differences are large enough to have occurred by chance alone. Direct experimentation is still necessary, however, to demonstrate that competition is the underlying causal factor of the observed patterns (Lewin, 1983; MacNally, 1983)

Even when competition is important in a community, it is likely to affect mostly only species interactions at the level of a guild (Begon, Harper & Townsend, 1990). Even then, as the number of species in the guild increases, the impacts of alternative processes are likely to obscure the effects of competition and invalidate the simple null model that is being used to describe the guild (MacNally, 1983). The concept of the guild arose out of the need for a term to describe functional roles of groups of similar species in communities. By Root's original definition, a guild is a group of species that use the same class of resources in a similar way (Root, 1967). This definition is free of taxonomic constraint although guilds, by nature, will often reflect taxonomy. Morphological differences between taxonomically diverse species will be reflected in differences in foraging method that often reduce resource use overlap between the species (Simberloff & Dayan, 1991). There are problems with the use of the guild definition. It is a somewhat fuzzy concept with fairly arbitrary means of delineating membership. In this study, I will follow the recommendations of (Simberloff & Dayan, 1991). The same class of resources is the sum of the prey spectra of different predators. Limb morphology that reflects locomotor function and affects foraging behaviour, combined with knowledge of killing behaviour, will be used to circumscribe guild membership on the basis of using resources in a similar way. In addition, part of the guild definition used by (MacNally, 1983; MacNally & Doolan, 1986), that the species are both sympatric and synchronous in activity, will be used.

Tasmania, a 68,300 square kilometre island off the southern coast of mainland Australia supports the largest assemblage of marsupial carnivores in the world. For the purposes of this study, marsupial carnivores are defined as members of the lineage Dasyuroidea, including the families Dasyuridae and Thylacinidae, whose diet is comprised mostly of vertebrate prey species. The small, largely insectivorous species are not included. Until the decline and possible extinction of the thylacine this century, there were four species, the eastern quoll, *Dasyurus viverrinus*, the spotted-tailed quoll (southern subspecies), *D. maculatus maculatus*, the Tasmanian devil, *Sarcophilus harrisii*, and the thylacine, *Thylacinus cynocephalus*. The two species of quolls and the devil are the largest members of the Family Dasyuridae and the largest remaining marsupial carnivores in the world. The thylacine is in a different Family, the Thylacinidae. The last confirmed sighting of a thylacine in the wild was in 1933 (Pearse, 1976). The two families that diverged some six to ten million years ago are in the Superfamily Dasyuroidea, a uniquely Australian group of marsupials (Clemens, Richardson & Baverstock, 1989; Dixon, 1989). All of these species exhibit pronounced sexual size dimorphism. With substantial differences in morphology between the sexes, there is the potential for intraspecific niche differentiation, so throughout this study sexes will be treated as separate morphospecies. Mean body masses are as follows: female eastern quoll - 0.7kg, male eastern quoll - 1.1kg, female spotted-tailed quoll - 1.7kg, male spotted-tailed quoll - 3.2kg, female devil - 5.4kg, male devil - 8.4kg and the thylacine - about 25kg (separate weights do not exist for males and females) (Dixon, 1989). Weights for the quolls and the devil are from this study. Because the thylacine declined before any ecological field studies were done, it is only included in analyses of skeletal material.

The four species of large dasyuroids in Tasmania are defined as a guild firstly on the basis that the bulk of the biomass of their diet comprises vertebrate prey,

primarily mammalian species. Secondly, they share similar limb morphology and hence locomotor function, leading to broad similarities in foraging behaviour. All species are digitigrade with non-retractile claws, although the granulated pad or calcaneum extends the full length of the carpal region and tarsus to the ankle and heel, which sometimes contact the ground when the animal is moving slowly. Compared to felids and canids, the dasyuroids are all short-legged and relatively slow moving. Also, they all have elongated rostrums, similar dentition and exhibit unspecialised killing behaviour. Uniformity in relative proportions between skull, axial skeleton and limbs is maintained across the larger carnivorous marsupials (Keast, 1982), and on skull dimensions *Dasyurus*, *Sarcophilus* and *Thylacinus* group together, distinct from the families of eutherian carnivores (Werdelin, 1986). Thirdly, all the species are active sympatrically and synchronously at night. Although there is justification in foraging behaviour for inclusion in the same guild, the degree of similarity varies within this guild. As expected this relates to taxonomic affinity. For example, the two congeneric species of quolls are much more similar in killing behaviour to each other than they are to the confamilial devil or the con-superfamilial thylacine. This is a good demonstration of the problems of guild definition (Simberloff & Dayan, 1991). To deal with this problem comparisons will be made, where appropriate, both across the entire guild and between the family and genus groupings of species within the guild. There are other vertebrate carnivores of mammalian prey in Tasmania. There are both large and small raptors, owls, and large elapid snakes. These were excluded from the guild because their foraging methods are so different. The smaller species of dasyurids, the marsupial mice, *Antechinus spp.* and *Sminthopsis*, are also excluded from the guild because their diet is primarily insectivorous.

This guild of dasyuroids or marsupial carnivores in Tasmania provides an excellent opportunity for studies of guild structure and comparative studies with eutherian carnivores. As a temperate island Tasmania has a discreet and depauperate vertebrate fauna in terms of species richness. It is thus a simple system to study with few other vertebrate carnivores and a limited number of prey species. The study of dietary overlap is made clearer than if many species were involved. Also, distributions of some of the Tasmanian dasyurids extend to the mainland providing the opportunity for natural experiments where one or more species is eliminated.

An ideal opportunity exists here to examine the ecological convergence of mammalian carnivores within the context of different evolutionary histories and physical environments. Australian marsupials have evolved in isolation to eutherian mammals for most of their evolutionary history and yet there are some remarkable convergences in functional roles and in many cases in morphology between the two groups. This is especially evident in the marsupial carnivores (Eisenberg & Leyhausen, 1972).

The overall aims of this study are: to describe the structure of the guild of the large marsupial carnivores in Tasmania in terms of relative abundance, morphology, trophic structure and habitat use and relate this to underlying causal factors; to determine the importance of competition as a structuring force in the guild; and to evaluate the relative importance of evolution and the physical environment in determining the composition of Australia's marsupial carnivore fauna. These aims

will be achieved by 1) searching for evolutionary evidence of competition (the "ghost of competition past") in morphological size relationships 2) seeking ecological evidence of exploitative competition in resource use overlap 3) finding other aspects of niche differentiation by which competition between the carnivores might be reduced 4) examining evidence of current interference competition and 5) comparing the composition of the Australian marsupial carnivore fauna with eutherian carnivore faunas on other continents in terms of differences in diversity of species and eco-morphological (diet/locomotor) types and relating this to differences in evolutionary history and the physical environment. Because these are large mammals, experimental manipulations of populations are not feasible within the scope of this study. Therefore, resource use overlap determined in this study may be used to predict the existence of current competition but direct evidence of competition cannot be demonstrated.

A field study site was chosen at Cradle Mountain in northern Tasmania. This site was selected because: it supported workable, sympatric populations of the three extant species of large dasyuroids, it provided a mosaic of vegetation types an advantage for the study of habitat use differentiation, was remote from farms and habitation where domestic livestock would influence the diet, was protected from logging activities and 1080 poisoning programs and provided good access and logistic support. A description of the study area follows.

1.2 Study Area

The study was conducted in a twenty square kilometre area, known as Cradle Mountain, at the northern end of the Cradle Mountain Lake St.Clair National Park in northern Tasmania (grid ref. 145°56'E, 41°36'S). This naturally defined area of sub-alpine forests and moorlands, the southern two-thirds of which is inside the National Park and World Heritage Area, is bounded by alpine plateau to the south, extensive buttongrass (*Gymnoschoenus sphaerocephalus*) moorlands to the west, the rugged Dove River canyon to the east and extensive sparse forest and grasslands under low intensity logging and grazing to the north. Elevation extends from 760m to 1080m, with the alpine area immediately to the south extending to 1545m (Cradle Mountain). The area encompassed the glaciated valley of the Dove River and part of the Iris River, which flow north into the River Forth and Bass Strait.

Cradle Mountain experiences a cold, wet climate. Climatic conditions during the study are outlined. Summer, the warmest months being from December to March, had a mean maximum temperature of 16°C (range 6 to 33°C). Winter, the coldest months from June to September, had a mean minimum temperature of 0.7°C (range -8 to 12°C). Prevailing weather from the south-west brings rain, sleet or snow two days out of three year round. Mean annual precipitation is 2368mm (range 2310 to 2403 mm). Drier months are March and April. Snowfalls are frequent between June and November (mean 36, range 31-42, snow days per year) with one to three deep falls a year which lie on the ground for three or four weeks. Weather is recorded daily at 8am by the National Park staff at the Cradle Mountain Visitor Centre (elevation 800m). Daylight hours change dramatically from the summer solstice (8 hour night) to the winter solstice (15 hour night).

Vegetation in Cradle Mountain is a mosaic of rainforest communities, eucalypt-dominated communities, lower altitude treeless vegetation (mainly buttongrass moorland) and alpine communities (Kirkpatrick & Mackie, 1991). These blocks of habitat are small, rarely more than one kilometre in minimum diameter and often 100m or less in extent. Rainforests and wetter eucalypt forests, both with clear, mossy understoreys, dominated south-facing slopes while north-facing slopes were characterised by eucalypt forests and woodlands with scrubby understoreys. For the purposes of this study, vegetation was classified as rainforest (cool temperate rainforest dominated by myrtle beech, *Nothofagus cunninghamii*, King Billy pine, *Athrotaxis selaginoides*, or pencil pine, *Athrotaxis cupressoides*; understorey usually clear and mossy), wet eucalypt forest (canopy of *Eucalyptus delegatensis*, *E. gunnii* or *E. coccifera* trees with a closed shrub layer that is clear and mossy at ground level + 1m), dry eucalypt forest (eucalypt canopy with closed, scrubby, shrub layer at ground level + 1m), mixed forest (includes *Leptospermum* and *Richea* scrub; closed stands, dense at ground level often on rainforest edges and stream banks), grassland (low *Poa* grasslands or herbfields dominated by *Gunnera cordifolia* or alpine coral fern, *Gleichenia alpina*) and buttongrass moorland (*Gymnoschoenus sphaerocephalus*; hummocks to one metre high).

Twenty-three species of mammals are known to have occurred at Cradle Mountain during the study, including three domestic species and two feral introduced species (Anon., 1988). In addition, the thylacine, now probably extinct, was well known from this area. Most Tasmanian mammals are represented, notable exceptions being the bandicoots (*Perameles gunnii*; *Isoodon obesulus* - present but rare), the long-nosed potoroo (recorded as rare in the National Park but never seen or recorded in scats during this study), the Tasmanian bettong, *Bettongia gaimardi*, the eastern grey kangaroo, *Macropus giganteus*. The broad-toothed mouse, *Pseudomys fuscus*, possibly occurs in the buttongrass areas, but since trapping records for this species are sparse and the fur is indistinguishable from that of its congener, the long-tailed mouse, *Pseudomys higginsi*, no definitive records of this species exist at Cradle Mountain. No systematic survey of any of the fauna was conducted during the study. The mammals recorded in Cradle Mountain during the study are in *Table I.I.* Seventy-six species of birds have been recorded in the Cradle Mountain Lake St. Clair National Park (Anon., 1988) but only twenty nine species were recorded in Cradle Mountain during the study, including one introduced species, the kookaburra. Only three species of reptiles were recorded on the study area during the project, the metallic skink (*Niveoscincus metallicus*), the white-lipped snake (*Drysdalia coronoides*) and the tiger snake (*Notechis ater*). Other species of specialised alpine skinks almost certainly occur at higher altitudes to the south of the study area. Three species of frogs were regularly heard calling in Cradle Mountain, the brown tree frog (*Litoria ewingi*), the brown froglet (*Ranidella signifera*) and the Tasmanian froglet (*Ranidella tasmaniensis*). Introduced brown trout (*Salmo trutta*) and native galaxid fish (*Galaxias spp.*) are in the Dove River and large invertebrates, the terrestrial crayfish *Parasticoides tasmanicus* and the freshwater crayfish *Astacopsis tricornus*, are present. Carnivores other than the devil and quolls include feral cats (six individuals were sighted, but only two were trapped or shot during the study), occasional escaped hunting dogs, raptors, owls, kookaburras (uncommon), tiger snakes, and whip snakes.

Human impacts in Cradle Mountain include a road running the full length of the valley, the National Park infrastructure (including visitor centre and walking tracks), a large campground, tourist accommodation in the Waldheim Cabins and the Cradle Mountain Lodge, an airstrip, roadhouse and an associated resident population of about 80 people. In peak season in January, more than 1,200 visitors a day enter the park. Human activities likely to affect the devils and quolls were: the road and tracks which animals sometimes used for straight line travel (spool and tracking demonstrated these were not used routinely or frequently), road mortality, year-round feeding of possums, pademelons, devils and quolls at the Cradle Mountain Lodge as tourist entertainment (this resulted in inflated populations of possums but the amount of food available for the carnivores, while constant, was very small), infrequent

Table 1.1 Mammals known to inhabit Cradle Mountain during the study. Bats are not included. Status has been determined from observation and from (Anon., 1988). Nomenclature follows (Smith, 1990).

Species			Presumed status
platypus	*Ornithorhynchus anatinus*		common
echidna	*Tachyglossus aculeatus*		sparse
swamp antechinus	*Antechinus minimus minimus*		sparse
dusky antechinus	*Antechinus swainsonii swainsonii*		sparse
spotted-tailed quoll	*Dasyurus maculatus maculatus*		sparse
eastern quoll	*Dasyurus viverrinus*		common
Tasmanian devil	*Sarcophilus harrisii*		common
southern brown bandicoot	*Isoodon obesulus affinis*		rare
common wombat	*Vombatus ursinus tasmaniensis*		common
sugar glider	*Petaurus breviceps breviceps*	(possibly introduced)	sparse
common ringtail possum	*Pseudocheirus peregrinus viverrinus*		common
brushtail possum	*Trichosurus vulpecula fuliginosus*		common
eastern pygmy possum	*Cercatetus nanus nanus*		rare?
Bennett's wallaby	*Macropus rufogriseus rufogriseus*		common
Tasmanian pademelon	*Thylogale billardierii*		common
house mouse	*Mus musculus*	(introduced)	rare
long-tailed mouse	*Pseudomys higginsi*		common
swamp rat	*Rattus lutreolus*		common
dog	*Canis familiaris*	(introduced domestic)	occasional
cat	*Felis catus*	(introduced)	sparse
horse	*Equus caballus*	(introduced domestic)	six
cattle	*Bos taurus*	(introduced domestic)	rare

scavenging at cabins and campground and buildings occasionally used as den sites by devils (eg. under the dining room of the Lodge). Road-mortality became a major issue after the road into the valley was sealed as far as the Lodge. This three kilometre section of sealed road within the study area probably caused the local extinction of the eastern quoll and a dramatic decline in the devil population towards the end of the study.

The tourist accommodation and associated animal feeding, tracks and roads in the valley was not considered to have a significant effect on the diet or overall maintenance of the devils or quolls but probably had some effect on movement patterns and certainly affected mortality.

Chapter 2 Competitive character displacement among large dasyurids: morphological size relationships and prey size patterning

2.1 Introduction

When ecologically similar species evolve in sympatry, competition theory predicts that there should be a shift in the morphological characters that relate proximately to the way in which they compete (Lewin, 1983; Dayan *et al.*, 1992). Patterns in morphological size relationships among coexisting competitors are seen as indirect evidence for competition (Simberloff & Boecklen, 1981; Greene, 1987). However, many factors select for size (Peters, 1983). The experimental manipulations required to demonstrate that competition is the underlying mechanism are difficult to execute on an evolutionary time scale. This has been demonstrated with beetles but is only feasible for animals with a short generation time (see Taper & Case, 1992)

Three size relationships have been investigated for patterns. For size ordered species in local guilds, it would be expected that (1) size ratios of linear dimensions related to feeding ecology should conform to a difference of 1.3, the Hutchinsonian ratio (Hutchinson, 1959), (2) these minimum ratios should be larger than expected by chance or in allopatry and (3) ratios of sizes of adjacent species should be more regular than expected by chance alone in order to more effectively partition food resources and reduce competition (Taper, 1993). The existence of Hutchinsonian ratios has only been weakly supported but the regularity of size ratios, also referred to as morphological patterning, included under the umbrella of character displacement has been controversial.

Brown and Wilson (1956) first used the term 'character displacement' in 1956, although the less restrictive definition of Grant (1972) is now in use. Character displacement is "the process by which a morphological character changes by natural selection arising from the presence in the same environment of ecologically similar species". Conversely, character release is a morphological change in the absence of a presumed competitor.

Many cases of character displacement were published during the 1970's and 1980's. However, with an upsurge in direct experimentation, as opposed to the collection of observational data, and application of the Popperian approach to science, requiring hypothesis falsification (Lewin, 1983), it was only in the early 1980's that suitable null hypotheses and statistical tests were developed to validate these claims. Strong, Szyka and Simberloff (1979), Roth (1981) and Simberloff and Boecklen (1981) found that very few claimed instances of character displacement stood up to statistical analysis.

Since 1959, when Hutchinson suggested using skull length as an appropriate measure in mammals for reflecting feeding ecology, more recent authors have gradually refined the trophic characters that have been measured to test for character displacement to those more closely related to feeding ecology (review in Dayan *et al.*, 1992). Schoener (1984) used wing length in investigating the size relationships among sympatric hawks because wing length is thought to be a more reliable indicator of feeding ecology in raptors than bill length, which is the most commonly used measurement in birds. Within mammals, Kiltie (1984; 1988) studying felid assemblages searched for patterns in jaw length, bite force, relative maximum gape and body length and mass. Their results suggested a tendency towards regularity but did not reach statistical significance. Malmquist (1985) demonstrated character displacement in two similar species of shrews in sympatry based on jaw dimensions. Dayan *et al.* (1989a; 1989b; 1990; & 1992) have refined the trophic features measured even further to the teeth, which are proximately related to feeding ecology. They demonstrated character displacement in both felids and mustelids in canine diameter , a character that relates directly to killing behaviour in these highly specialised killers (Dayan *et al.*, 1989a; 1990). Lower carnassial length was the trophic character that exhibited regularity of size ratios in canids (Dayan *et al.*, 1989b; 1992; Dayan & Simberloff, 1994). This result is not as easy to explain and a direct demonstration of the role of the carnassial teeth in killing and feeding behaviour in these relatively unspecialised predators is needed. Character release has been demonstrated in mustelids and canids in geographic areas with fewer species than those areas where character displacement is evident (Dayan *et al.*, 1992; Dayan & Simberloff, 1994).

If the observed regularity of size ratios is a coevolutionary response to reduce competition for food resources then some evidence that tooth size does correlate with prey types utilized is required. Vucetich *et al.* (manuscript) extended Dayan *et al.* (1989a) work on North American mustelids to include two larger species and examined their prey size utilization by the same statistical technique used to detect morphological size patterning. They found no support for an ecological or competitive basis for the competitive character displacement hypothesis. There was no evidence of patterning in prey size or of dietary differences that correlated with the observed patterning in trophic characters. Dayan & Simberloff (1994) found empirical support for the hypothesis of prey size partitioning in published data on diet of the British mustelids. Body size and prey size are correlated and there are sex-related differences in diet.

In recent reviews, (Taper & Case, 1992; Taper, 1993) concluded that patterns of size regularity are neither universal nor rare and ask why they occur in some local guilds but not in others. This question has been taken up by Hopf and Hopf (1985) and Hopf, Valone and Brown (1993) who have developed a theory of the costs of commonness and rareness and the effects of these on community structure. Their approach is to examine other factors besides resources which may affect competing species (Taper, 1993). These factors include internal population dynamics and community interactions such as predation, parasitism and disease.

Data on body weight collected during the early part of the field component of the project indicated an apparent equal spacing in body mass when fully grown adult

males and females were treated as separate morphospecies (*Figure 2.8*). This indicated that character displacement in structures closely related to feeding behaviour may be occurring. Food is the resource most likely to be in limiting in this guild (potentially limited resources are discussed in more detail in Chapter 3).

The aims of this study are to test whether (1) character displacement, in the form of a regularity of size ratios among adjacent morphospecies, occurs in trophic structures that are proximately related to feeding ecology among the marsupial carnivores in Tasmania, (2) patterns of prey size of the carnivores correlate with the observed morphological patterns (3) character release occurs on the south-eastern mainland of Australia where the two larger species, the devil and thylacine, have been absent for a significant number of generations (4) character displacement occurs in the different species assemblage of quolls in Queensland and (5) what other factors, such as latitudinal size gradients or sexual selection, influence body size?

To test for morphological patterns in the Tasmanian carnivore guild, the species were divided into three groupings of increasing taxonomic and morphological diversity. Tests were conducted among congeners (the eastern quoll, *Dasyurus viverrinus*, and the spotted-tailed quoll, *D. Maculatus maculatus*), members of the Family Dasyuridae (the two species of quolls and the devil, *Sarcophilus harrisii*) and across all four large species in the Superfamily Dasyuroidea (two quoll species, devil and the thylacine, *Thylacinus cynocephalus*). Morphological characters were measured on museum specimens hence the thylacine was included in analyses, but information on prey size was collected at the study area at Cradle Mountain in northern Tasmania.

Four geographic areas with different species assemblages of large dasyuroids were examined (1) Tasmania, with four species analysed in three separate species combinations, (2) the south-eastern mainland of Australia, within the distributional range of the eastern (*D. viverrinus*) and spotted-tailed quolls (*D. Maculatus maculatus*) but where devils and thylacines are absent, (3) south-east Queensland, which is the extreme northern limit of the range of the southern subspecies of the spotted-tailed quoll (*D. maculatus maculatus*) and the extreme southern limit of the range of the northern quoll (*D. hallucatus*), and (4) north-east Queensland, where the northern subspecies of the spotted-tailed quoll (*D. maculatus gracilis*), and the northen quoll occur in sympatry.

2.2 Methods

2.2.1 Morphological patterns

2.2.1.1 Morphological characters

Measurements were taken from skulls in the Tasmanian Museum and Art Gallery in Hobart, the Queen Victoria Museum in Launceston, Tasmania, the Museum of Victoria, Melbourne, the Donald Thomson and the Department of Fisheries and Wildlife Collections housed at the Museum of Victoria, the Australian Museum,

Sydney, the Macleay Museum of the University of Sydney, the Queensland Museum, Brisbane, the South Australian Museum, Adelaide and from private research collections (Scott Burnett, Menna Jones, Les Moore).

Only skulls from adults of known sex and locality were used. Skulls were judged to be adult by complete dental rupture and an assessment, based on extensive field experience, of a combination of size and tooth wear. Because dasyurids and presumptively also thylacinids produce only one set of teeth during their life, full dental rupture occurs when animals are still only two thirds of adult female size. There is no overlap in size between sexes of fully grown adult individuals of any of the three species. Therefore, skulls of males in the adult female size range were rejected because they had not reached their final adult size. All of the larger dasyurids and *Thylacinus* endure substantial tooth wear during their life. This is particularly noticeable on the canines and the lower M2 and M3. Tooth nomenclature follows Archer (1978). The four molar teeth of dasyuroids are M2 to M5. Dayan *et al.* (1989a; 1992) rejected skulls that had worn carnassials or canines. Unlike eutherian carnivores, the teeth of the larger marsupial carnivores continue to grow throughout life so tooth wear is compensated by tooth growth and canine length and diameters actually increase with age (Jones, in prep.). Therefore, teeth were rejected for measurement only if they were broken or worn to stumps. Specimens were pooled from large geographic areas to ensure adequate sample sizes. This may have masked some latitudinal gradients in size. Means of characters measured on *D. maculatus* and *D. viverrinus* skulls from the northern and southern areas of the large south-eastern Australian range did not differ significantly so pooling of the data was valid and did not mask any latitudinal size gradients (one-way AOV and Tukey's HSD on each character for both species, all p values >0.05).

Nine characters were calculated, from eleven skull measurements, that were considered to relate directly to feeding ecology (*Figure 2.1*).

Body size was estimated from condylo-basal length (CBL) (von den Driesch, 1976) and basicranial axis length (BCAL) (Radinsky, 1984). Body weight was not used because it is not a good measurement of body size. It changes with seasonal variation in body condition and is rarely recorded with older museum specimens. Skull length or CBL is the most commonly used standard for body size against which other measurements are compared. Also specimens of skulls in museums usually lack the post-cranial skeleton from which other size measurements can be taken. Radinsky (1984) concluded that for comparisons across species, a measure of skull length independent of variations in face length was appropriate. In case the selection of standard measurement influenced results, analyses were repeated using both CBL and BCAL as body size standards. Preliminary analyses showed no differences between the two measures so CBL was used as the standard size measurement in all final analyses.

The maximal anterior-posterior diameter of an upper canine (CMD) was measured for canine size. Canine strength in bending about the anterior-posterior and medio-lateral diameters (Sx and Sy respectively), were calculated from CMD, the maximal medio-lateral diameter and the crown height of an upper canine using the method in Van Valkenburgh and Ruff (1987). This calculation involves modeling the

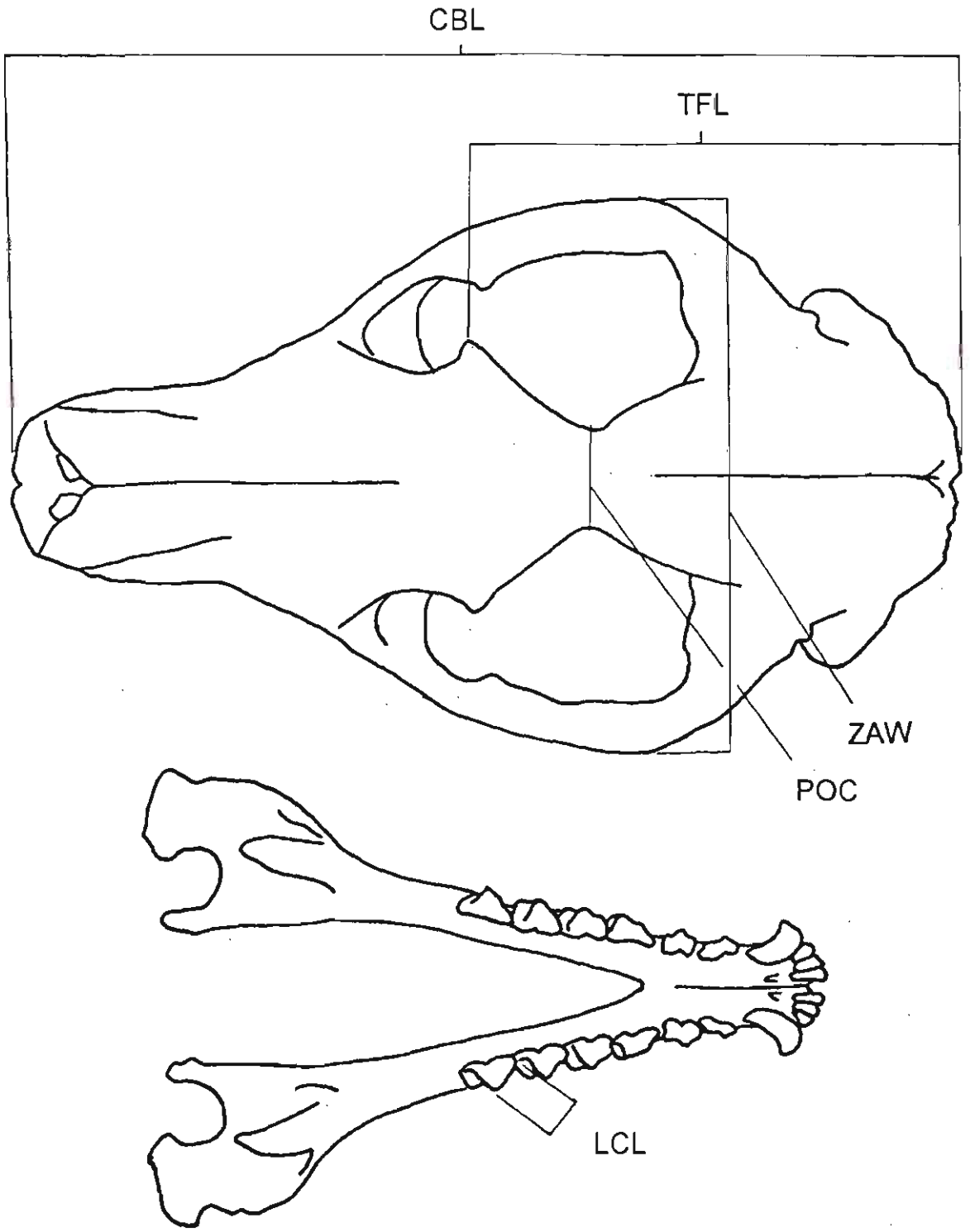


Figure 2.1 Characters measured on dasyuroid skulls that were used for analysis of character displacement. CBL = condylobasal length; TFL = temporal fossa length; ZAW = zygomatic arch width; POC = post-orbital constriction; LCL = lower carnassial length

upper canine as a cantilever, a solid beam with an elliptical cross-section, fixed at one end. Because tooth growth in dasyuroids is continuous, the dentine-enamel junction in old individuals has sometimes grown out to almost the tip of the canine. Therefore, crown height of the canine was measured from the junction of tooth with the skull instead of dentine-enamel junction as is used in eutherian carnivores (Van Valkenburgh & Ruff, 1987).

Measurement of the length of the lower carnassial (Dayan *et al.*, 1992) was adapted for dasyuroids because their dentition is not equivalent to that of eutherian carnivores. Marsupial carnivores lack a specialised carnassial tooth, the four lower molars, M_2-M_5, being reasonably similar in structure (Archer, 1976; Archer, 1978). However, the paracristid crest connecting the paraconid to the protoconid forms the functional equivalent of the shearing blade and carnassial notch. This crest is on the outer, anterior face of the lower molar tooth, similar in position to the eutherian carnassial blade. As the degree of carnivory increases in the Dasyuridae from the smallest and most insectivorous quoll, *Dasyurus hallucatus*, to the completely carnivorous *Sarcophilus*, the paracristid becomes longer and more longitudinally oriented at the expense of the reduced metacristid (this is discussed in detail in Chapter 6). Bensley (1903, in Archer, 1976) comments that the effect of this is to increase the importance of the shearing function and line up the shearing crests of individual teeth to create one long shearing unit. This is functionally equivalent to an enlarged carnassial tooth. Although the four lower molars are similar in structure, they have different functions. The effective carnassial tooth is the posterior-most molar, M_5. It is in the equivalent geometrical position along the ramus to the M_1 carnassial in eutherians (Werdelin, 1986). Also, it should be noted that this tooth is the last tooth to become worn in old animals and remains sharp throughout the life of most individuals, thereby retaining its shearing function (see Chapter 6). The measurement for lower carnassial length, M_5L, was taken as shown in *Figure 2.1*. Although thylacines are dentally distinct from dasyurids (Archer, 1976), they are similar enough that the same measurements apply.

An index of temporal muscle size, which affects bite strength at the canines, (Radinsky, 1981a) was calculated by $\sqrt{(TFL*(ZAW-POC))}$ where TFL is temporal fossa length, ZAW is zygomatic arch width and POC is the diameter of the post-orbital constriction (definitions after Radinsky, 1981a) (*Figure 2.1*). Dayan *et al.* (1990) and Vucetich *et al.* (manuscript) used ZAW as a simple index of temporal muscle size.The more complex measurement used in this study for the dasyuroids is justified by the different relative sizes of the brain case. *D. viverrinus* had the largest brain case relative to body size resulting in a large measurement for the post-orbital constriction while *S. harrisii* had the smallest brain case and a very narrow post-orbital constriction. Even if the ratio of ZAW to TFL was constant in all species, the size of the brain case which determines the diameter of the post-orbital constriction would vary the size of the space available for the temporalis muscle.

Bite strength at the carnassials was compared by measuring the moment arm of the masseter, MAM, and masseteric fossa length, MFL (Radinsky, 1981a). The relative contribution to bite strength is unknown but MAM indicates the mechanical advantage of the deep masseter and MFL reflects its size (Radinsky, 1981a; Werdelin, 1986).

Measurements were taken to 0.01mm precision with vernier calipers. Measurement error is expected to be low because the measurement points are well defined and the bone material being measured is hard. For three measurements, TFL, MAM and MFL, these points are not well defined and the values will not be precise. Because skulls get broken and teeth go missing, the number of measurements for each character will not always match.

A high degree of correlation could be expected between the characters because they are all skull measurements, and the large number of characters measured would result in a very small critical p-value in statistical analyses (see 2.2.1.2). A Principal Components Analysis (PCA) and Pearson's product-moment correlation were run to identify correlated groupings of characters. The PCA produced no useful patterns beyond finding a size correlation among all the characters. Pearson's Correlation matrix demonstrated that all characters were correlated with each other ($r>0.7$) except for Sx with BCAL. The number of characters selected for analysis was reduced to five on the basis, then, on the perceived importance of their biological function and their distinctiveness of function. CBL was selected as a measure of body size, APD for canine size, Sx for canine strength in the direction of most force, SMA for muscle force at the canines and LCL for carnassial length. The measures of force at the carnassials, MAM and MFL, were both discarded because they were more closely correlated with SMA, temporal muscle size, than they were with carnassial length, LCL.

In addition to the morphological characters measured on skulls from museums, mean values for body mass and some morphometrics were calculated for each morphospecies at the field study site at Cradle Mountain. The trapping regime is outlined in Section 2.2.2.1. Each individual was weighed on its first capture for each trip using Salter 10kg spring scales accurate to 0.005kg. All body weights of each individual weighed during the field study were combined so that the mean values represented both intra- and inter-individual variation in body mass. The large number of body mass measurements taken for each individual validated the use of mean body mass of each morphospecies in analyses as a measure of body size (Freeman & Jackson, 1990).

Each individual was measured just once a fully grown adult. Head length, head width, hindleg (a bone measurement from the top of the tibia to the base of the heel) and pes (a very precise measure, different from the traditional measurement, taken from the distal end of the metatarsals to the back of the heel) were measured with vernier calipers to 0.01 mm precision. Neck and girth circumferences were measured with a tape measure to 0.5 cm accuracy. Head length, head width, hindleg and pes were the easiest and most precise measurements to take in the field on unanaesthetised animals. Of these, pes was the most precise. To determine which external body measurement was the best predictor of overall body size for each species, a Principal Components Analysis was performed on the complete set of measurements minus the specific measurement being tested. The score of the unrotated first axis for each individual was then used as a variable repesenting overall size. Regression analyses of each type of measurement and the first PCA axis were used to determine if this particular measurement was a good predictor of overall body size. Head length, head width, hindleg and pes were tested separately. Because

of small sample sizes, sexes were pooled for each species. Head width was the best measure of overall body size of eastern quolls, pes was the best for spotted-tailed quolls and hindleg for devils. Results of regression analyses are in *Table 2.1*. Of the three measures that represented body robustness, head width, neck circumference and girth circumference, a PCA and Pearson's correlation matrix indicated that neck circumference would be the best estimator across all three species.

Table 2.1 Results of analyses of three external body measurements representing body size regressed against the unrotated principal factor scores from PCA of all other body measurements (r^2_{adj}).

	N	Head length	Head width	Hindleg	Pes
Dasyurus viverrinus	21	0.661	0.763	0.115	0.653
D. maculatus maculatus	12	0.783	0.688	0.726	0.796
Sarcophilus harrisii	41	0.529	0.240	0.705	0.556

2.2.1.2 Statistical analyses for detecting morphological patterning

Morphological patterning in the form of equal size ratios among adjacent morphospecies was tested for each character using the Barton-David (B-D) Test (Barton & David, 1956). There are several tests that determine whether a series of points break a line into independent, random segments or not (reviews in Tonkyn & Cole, 1986; Dayan *et al.*, 1990). There has not been any analyses of the relative power of these tests (Dayan *et al.*, 1990; Dayan *et al.*, 1992) but Simberloff (1989) discusses the merits. I used the B-D test because it is a simple and accurate test for detecting whether two points on a line and corresponding a size ratio are too small to have occurred by chance (Boecklen & NeSmith, 1985; Dayan *et al.*, 1990), and for compatibility with recent studies (Dayan *et al.*, 1989a; 1989b; 1990; 1992; Vucetich *et al.*, manuscript).

Given that the difference of the logarithms of means is equivalent to the ratio of the means, if the difference of the logs of means of a character from adjacent morphospecies are ranked from smallest to largest, various combinations of differences (ratios) can be tested to determine if they are too small or large to have occurred by chance. The null hypothesis of random spacing of sizes of morphospecies in an assemblage is falsified if size ratios are remarkably evenly spaced. I tested the smallest to largest ratio G_{1n}, second smallest to largest G_{2n} and the smallest to the second largest $G_{1(n-1)}$. The details of the application of the B-D test are outlined in Barton & David (1956) and Simberloff & Boecklen (1981).

Several valid criticisms have been directed at the B-D test. Tonkyn & Cole (1986) stated that the underlying size distribution for the null model, of competition not being responsible for size patterning, is not known and may be affected by many other factors. Also, the natural endpoints for the largest and smallest possible sizes or

the constraints (eg. physiological) on sizes are not known. By using the largest and smallest species as these endpoints creates the problem that the intermediate points are not independent. Criticisms have also been made that the use of a log-uniform distribution incorporates aspects of the hypothesis (of ratio constancy) into the model and thus increases the type I error rate, the chance of detecting a pattern when there isn't one. Boecklen & NeSmith (1985) defended the use of log-uniform distributions and found that the B-D test is slightly liberal for small species assemblages, that is the Type II error rate or chance of missing and effect is high, but the difference is small and would have little effect on hypothesis testing. The test then errs on the side of caution. However, the B-D test should be viewed as a descriptive statistic of patterns in the data rather than a rigorous test of a hypothesis (Dayan *et al.*, 1992).

When a group of conceptually related tests are analysed, the probability that any one test will be statistically significant increases with the number of tests in the set. The Bonferroni technique controls this Type I error rate, the possibility of falsely declaring one or more tests significant. However it assumes complete intercorrelation of the tests and is thus conservative for all tests except the one that yields the lowest probability (Dayan *et al.*, 1992). All the tests are correlated, but they are not completely correlated. To overcome this problem, both the Bonferroni and a multi-stage testing procedure designed for completely independent tests (Rice, 1990) were used. In practice, the difference was trivial.

2.2.2 Dietary patterns

2.2.2.1 Collection of scats

Scats for dietary analysis were obtained from animals trapped, and released at point of capture, between October 1990 and April 1993 at Cradle Mountain. Each scat is identified with an individually marked (tattooed) individual of known sex, age/size class, reproductive and body condition.

Devils, spotted-tailed quolls and eastern quolls were trapped overnight in specially constructed wire cage traps baited with beef liver, a bait that left no remains in the scat that could confuse dietary analysis. Trap design (Jones, in prep.) overcame previous problems with trapping devils. Traps were O.7m in length, longer than the usual 0.5m, with light aluminium guillotine doors that had a folded edge on the bottom. This prevented large devils or spotted-tailed quolls from leaving their tail tip in the door as it closed and either losing it or escaping from the trap. Wire mesh used in trap construction was a fine gauge and not very strong. Devils were generally unable to get a purchase on the mesh with their teeth but if they did it bent and they did not risk breaking their canine teeth, important when the animals were being released back to the wild. Wire hooks were used because devils learn to remove bait, even if wired on, from treadle traps without getting caught. The rear of the trap was solid sheet aluminium designed to direct animals towards the front door. Devils sometimes set off a trap by digging around the sides and rear where the bait smell is strongest.

Heavy plastic sheeting was placed over the rear two-thirds of the trap as protection against the weather. This also helped direct animals towards the entrance. Plastic and trap was then secured using tent pegs and rocks or logs, ensuring the trap floor was stable to walk on when animals entered. This also reduced the liklihood of a devil setting the trap off by digging. No problems were experienced of animals from suffering exposure in the severe climate at Cradle Mountain. Care was taken that the trap was not on ground liable to become waterlogged. A handful-sized piece of bait, enough to provide an eastern quoll with a night's sustenence, was provided. The larger species were considered to be more robust to the cold and less likely to suffer from energy depletion as a result of lack of food.

Traps were placed along paths, creeks and forest verges especially where there was evidence of animal activity. The trap was bedded in firmly with the entrance closest to the logical approach route, the rear of the trap being pushed into a dense bush or obscured by logs. Sixty traps were spread over fifteen square kilometres. Because carnivores have large home ranges and are relatively scarce, traps were set, not on a grid, but by trial and error where animals were likely to be caught. All traps were more than 10m apart, although they were often clumped in areas of high capture success. Different trap environments worked for each species although a few trap situations would trap all three species. Devils were most frequently trapped in eucalypt forest along major thouroughfares such as roads and tracks. Both species of quolls were caught in traps set on forest verges when the rear of the trap was pushed into a dense bush such as cutting grass, *Gahnia sp.* Spotted-tailed quolls were frequently trapped in rainforest, in dense sclerophyllus understorey of eucalypt forest or near creeks. Eastern quolls were most commonly caught on forest verges adjacent to open grassland or moorland or in the open.

Traps were cleaned using water and a scrubbing brush after each capture. Quolls were generally not caught in traps fouled by devils. Traps were left in position to be cleaned by the weather between trips.

A maximum of thirty traps were set at a time and checking commenced at dawn. Two traplines of thirty traps each were set; one was low level, accessible by vehicle and could be set in bad weather and the other was high level entailing a seven kilometre walk. Each trapline was set for a maximum of three days per trip. This gave one hundred and eighty trap nights per trip and a useful number of captures without too many multiple captures of the same individuals. It also reduced the problem of devils working a trapline and attempting to eat the eastern quolls inside the traps. Trapping was carried out bi-monthly throughout the two-and-a-half years of field work, giving good coverage of all seasons.

2.2.2.2 Identification of prey items

Scats collected from traps were oven dried and stored in paper bags. They were later soaked in hot water and washed through 1mm and 0.1mm stacked sieves. The large components and sludge were stored separately in 70% alcohol. Mammalian prey were identified to genus or species level using cross-sections of fur (Brunner & Coman, 1974; Taylor, 1985). Identifications were confirmed and, where possible, larger species (possums, macropods and wombat) were classified as adult or juvenile by comparison of bone fragments in the scats with reference skeletons in the

Tasmanian Museum Art Gallery and diagrams in (Green & Rainbird, 1983). Avian prey were classified to order level, or species if they were distinctive (eg. rosella, currawong) using (Day, 1966) and a reference collection. Reptiles were classified to species using a taxonomically current key for Tasmanian reptiles (Swain, unpublished) and reference specimens (Roy Swain, Sue Jones). Crustaceans were identified to species level (by Alastair Richardson) and insects to order (CSIRO, 1991). Earthworms were detected in scats by microscopically examining the fine sludge for chaetae (Kruuk & Parish, 1981).

2.2.2.3 Statistical analyses for detecting patterns in prey size

To examine the hypothesis that prey size used by guild members is similarly patterned to morphological characters, the weighted mean prey mass for each morphospecies was calculated from mean mass for each prey species (Strahan, 1983; Slater, Slater & Slater, 1989) and total number of prey items of each species. The Barton-David test was used to test for patterning in the form of equal size ratios.

In addition, the analyses of prey size / body size patterns from Chapter 3 were used in interpretation of results.

2.3 Results

2.3.1 Latitudinal variation in size

Both male and female eastern quolls are significantly larger in size for all five characters in Tasmania than on the south-eastern Australian mainland (*Table 2.2*). There are no differences in the size of female spotted-tailed quolls (*D. maculatus maculatus*) between all three geographic regions where this subspecies occurs, except for lower carnassial length (LCL). Female spotted-tailed quolls in south east Queensland have longer carnassial lengths than those in the southeastern mainland which are larger than those in Tasmania, although only the difference between Queensland and Tasmania is significant (Tukey HSD, p=0.037). Male spotted-tailed quolls (*D. maculatus maculatus*) demonstrate latitudinal size variation in maximal anterior-posterior diameter of the upper canine (APD), canine strength (Sx) and LCL. Tasmanian animals are smaller than those on the south-eastern mainland for Sx (Tukey HSD, p=0.049) and smaller than those in both south east Queensland and south-eastern mainland for LCL (Tukey HSD, p<0.001 for both). Male spotted-tailed quolls in south east Queensland are smaller than those in the south-eastern mainland and in Tasmania for APD (Tukey HSD, p=0.006.and p= 0.041 respectively) and larger for LCL (Tukey HSD, p=0.005 and p<0.001 respectively) (*Table 2.2*; *Figure 2.2*).

A few spotted-tailed quoll skulls from King Island in Bass Strait, where they are now extinct, were found in the Queen Victoria Musem and measured. Consistent with expected results, they are larger than spotted-tailed quolls from any other geographic region (see Discussion). The results have not been included, however, because there is one female and one male that are so much larger than the rest of the

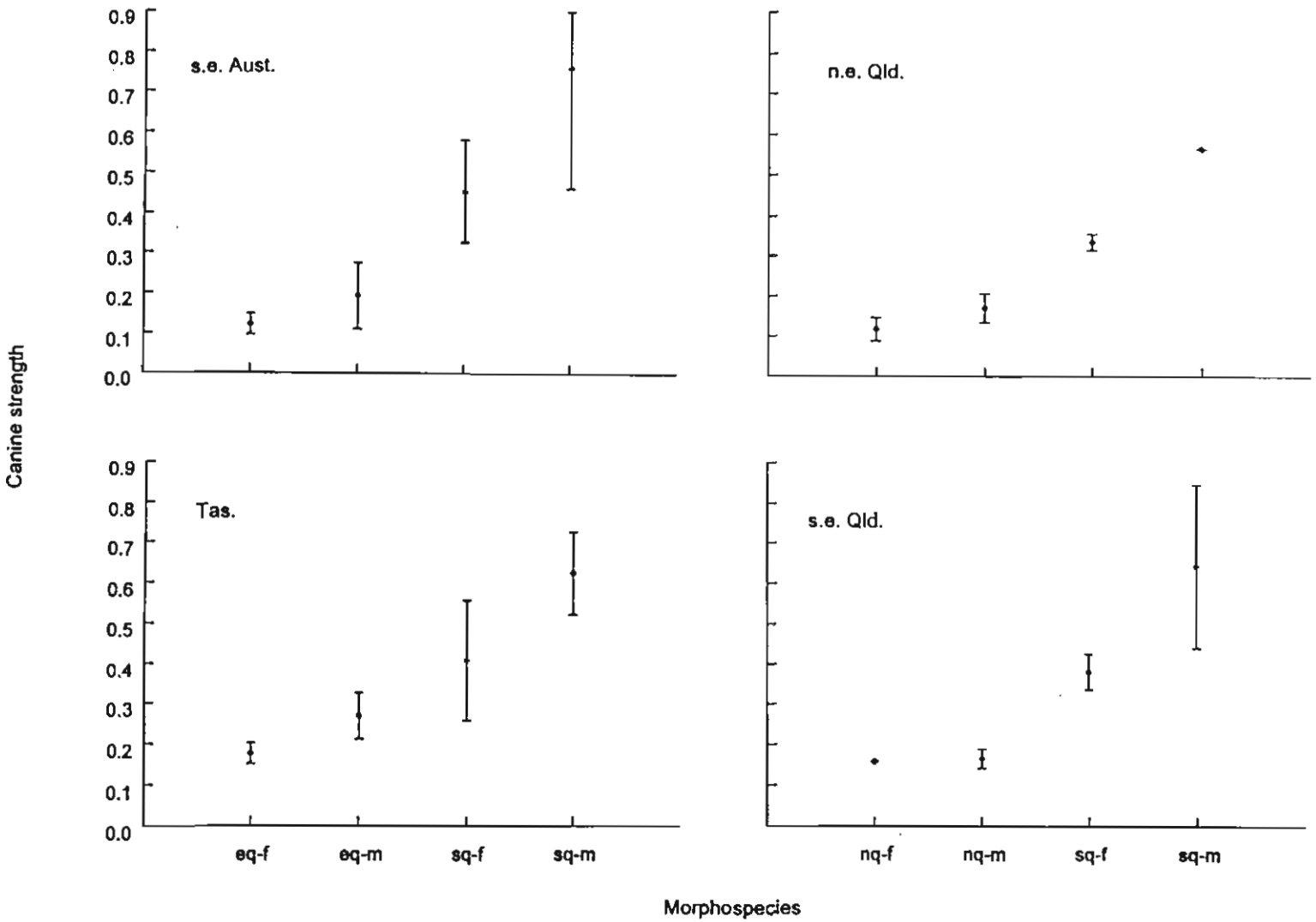


Figure 2.2 Canine strength (Sx) for quolls (Dasyurus spp.) in four geographic areas in Australia: Tasmania (Tas.), south-eastern Australian mainland (s.e.Aust.), south-east Queensland (s.e.Qld.) and north-east Queensland (n.e.Qld.). Morphospecies are as follows: f = female, m = male, eq = eastern quoll, sq = spotted-tailed quoll, nq = northern quoll. Note that the spotted-tailed quolls in Tasmania, the south-east mainland and south-east Queensland are the subspecies, *D. maculatus maculatus*, while the spotted-tailed quoll in north-east Queensland is the much smaller subspecies, *D. maculatus gracilis*.

Table 2.2 Latitudinal variation in size of morphological characters (in mm) and comparison of means by Students t-test or 1-way analysis of variance for the eastern quoll, *Dasyurus viverrinus*, and the spotted-tailed quoll, *D. maculatus maculatus*. Sample statistics are presented for the Tasmanian devil, *Sarcophilus harrisii*, and the thylacine, *Thylacinus cynocephalus*.

			Tas			s.e Aust			s.e. Qld				
			N	Mean	s.d.	N	Mean	s.d.	N	Mean	s.d.	t / F	p
Dasyurus	female	CBL	28	74.24	1.89	15	63.70	4.07				-9.501	<0.001
viverrinus		APD	29	3.23	0.26	18	2.55	0.30				-7.925	<0.001
		Sx	29	0.18	0.03	18	0.12	0.03				-7.113	<0.001
		SMA	28	32.46	1.93	15	29.04	2.23				-5.011	<0.001
		LCL	29	3.96	0.09	18	3.57	0.25				-6.531	<0.001
	male	CBL	50	81.62	3.59	22	69.28	5.82				-9.200	<0.001
		APD	52	3.91	0.41	24	3.23	0.40				-6.869	<0.001
		Sx	51	0.27	0.06	24	0.19	0.08				-4.028	<0.001
		SMA	51	37.05	3.06	22	32.66	3.21				-5.445	<0.001
		LCL	52	4.21	0.18	24	3.87	0.42				-3.739	0.001
Dasyurus	female	CBL	10	89.96	7.39	15	91.31	5.77	4	89.81	3.88	0.181	0.835
maculatus		APD	12	4.25	0.60	16	4.51	0.49	4	3.88	0.31	2.585	0.093
maculatus		Sx	12	0.41	0.15	15	0.45	0.13	4	0.38	0.05	0.736	0.488
		SMA	10	44.46	4.64	14	44.79	2.56	4	43.98	2.44	0.091	0.913
		LCL	12	4.89	0.25	16	5.00	0.27	4	5.27	0.20	3.406	0.047
	male	CBL	24	105.03	5.69	58	104.51	5.34	14	103.99	7.54	0.149	0.862
		APD	27	5.42	0.38	73	5.48	0.52	13	4.98	0.81	4.996	0.008
		Sx	27	0.62	0.10	73	0.76	0.30	13	0.64	0.20	6.234	0.001
		SMA	25	54.08	3.86	56	53.74	3.78	12	54.38	4.87	0.157	0.855
		LCL	27	5.16	0.18	72	5.39	0.20	14	5.58	0.20	23.289	<0.001
Sarcophilus	female	CBL	23	121.83	3.65								
harrisii		APD	23	8.92	0.66								
		Sx	23	2.72	0.33								
		SMA	23	71.40	3.78								
		LCL	23	10.38	0.28								
	male	CBL	20	132.59	5.31								
		APD	20	10.03	0.82								
		Sx	20	3.54	0.54								
		SMA	20	79.28	13.33								
		LCL	20	10.35	0.31								
Thylacinus	female	CBL	3	194.15	7.41								
cynocephalus		APD	4	9.36	0.11								
		Sx	4	1.91	0.12								
		SMA	3	77.74	2.81								
		LCL	4	11.49	0.19								
	male	CBL	3	232.30	4.65								
		APD	4	11.95	1.16								
		Sx	4	3.54	0.70								
		SMA	4	95.43	4.06								
		LCL	4	12.95	0.24								

specimens that they exert a strong influence on the means. With such small sample sizes, it is not possible to determine whether these two individuals are representative.

There are no differences in size between northern quolls from south-east or north-east Queensland for any characters although sample sizes are very small for the south-east. These results and sample statistics for the northern subspecies of the spotted-tailed quoll are in *Table 2.3*.

Table 2.3 Latitudinal variation in size of morphological characters (in mm) and comparison of means by Students t-test for the northern quoll, *Dasyurus hallucatus*, and sample statistics for the northern subspecies of the spotted-tailed quoll, *D. maculatus gracilis*.

			s.e. Qld			n.e. Qld				
			N	Mean	s.d.	N	Mean	s.d.	t	p
Dasyurus	female	CBL	2	62.55	4.40	10	60.67	2.10	-0.592	0.633
hallucatus		APD	2	2.69	2.52	10	2.36	0.25	-1.788	0.261
		Sx	1	0.15	0.24	8	0.12	0.03		
		SMA	2	30.11	2.01	10	27.31	1.74	-1.842	0.268
		LCL	2	2.68	0.20	9	2.76	0.14	0.544	0.669
	male	CBL	6	65.01	5.20	6	64.74	3.52	-0.104	0.919
		APD	5	2.89	0.29	6	2.89	0.29	0.008	0.994
		Sx	5	0.17	0.02	5	0.17	0.04	0.271	0.794
		SMA	2	30.11	2.01	6	31.20	2.91	-0.558	0.589
		LCL	2	2.68	0.20	6	2.93	0.09	0.000	1.000
Dasyurus	female	CBL				2	82.87	3.61		
maculatus		APD				2	3.97	.004		
gracilis		Sx				2	0.33	0.02		
		SMA				2	39.09	3.05		
		LCL				2	4.82	0.11		
	male	CBL				3	92.33	9.42		
		APD				3	4.29	0.36		
		Sx				3	0.41	0.14		
		SMA				3	44.77	7.27		
		LCL				4	5.09	0.17		

2.3.2 Sexual dimorphism

All five species of dasyuroids are significantly sexually size dimorphic (SSD) for all characters, except for lower carnassial length (LCL) in devils where females are slightly larger than males. Sexual size dimorphism is most pronounced for canine strength (Sx), less so for canine diameter (APD) and bite force at the canines (SMA) and least for skull length (CBL) and LCL in all species. (*Table 2.4*)

The degree of sexual dimorphism expressed in different characters varied between species and among geographic areas. In Tasmania, SSD for skull and trophic characters is greatest for the thylacine, almost equal between spotted-tailed quolls and eastern quolls although spotted-tailed quolls are slightly more dimorphic, and least for devils (*Table 2.4*). However, for external measurements, representing overall body size and robustness, from study animals at Cradle Mountain, spotted-tailed quolls exhibit a much greater degree of SSD than the eastern quolls or the

devils which are almost equal. Thylacines, of course. are absent from this analysis. Spotted-tailed quolls show one and a half times the degree of SSD in pes and neck circumference and almost twice the degree in body mass than the other two species (*Table 2.5*). SSD for northern quolls in north-east Queensland is intermediate between that of eastern quolls and devils. Very small sample sizes (n=2 for females in southern Qld) preclude any generalisations about latitudinal variations in this species (*Table 2.4*).

SSD for eastern quolls is more pronounced in the south-eastern mainland than in Tasmania for the tooth characters Sx, APD and LCL, but unchanged for CBL and SMA. For spotted-tailed quolls SSD for Sx is more pronounced on the south-eastern mainland than in Tasmania, is less pronounced for APD and unchanged for CBL, SMA and LCL. The consequences are that spotted-tailed quolls are more dimorphic for trophic characters than are eastern quolls on the mainland, the opposite to Tasmania. Spotted-tailed quolls in southern Queensland exhibit a similar degree of SSD to those in the southeastern mainland. The northern subspecies of the spotted-tailed quoll, *D. maculatus gracilis*, exhibits a much smaller degree of SSD than its larger subspecies, *D. maculatus* maculatus. It is equivalent to the devil in its small degree of size dimorphism in trophic characters. The lack of significant differences in size of characters between males and females is probably a consequence of very small sample sizes (two females and three males). (*Table 2.4*)

To determine whether the observed dimorphism in canine strength (Sx) is entirely a result of allometric scaling or, alternatively, whether males have stronger canines for their body size than females, canine strength is divided by skull length to correct for body size. Comparison of these arbitrary means by Students t-test show that males have stronger canines for their body size than do females for eastern quolls, spotted-tailed quolls and devils in both Tasmania and on mainland Australia (all $p<0.05$). This is not the case for the thylacine (t=-2.372, p=0.138). When this analysis is repeated on neck circumference, the external character that appears to differ most between the sexes, by dividing neck circumference by head width for eastern quolls, by pes for spotted-tailed quolls and by hindleg for devils (the best overall measures of body size for each species, respectively), only male spotted-tailed quolls have thicker necks for their body size than females (t=-3.774, p=0.003). There are no significant differences for eastern quolls (t=-0.-0.740, p=0.489) or for devils (t=-0.974, p=0.333).

Table 2.4 Percentage of sexual dimorphism (male/female) and comparison of means by t-test for the five species of dasyuroids.

		Tas			s.e. Aust			s.e.Qld			n.e.Qld		
		%	t	p	%	t	p	%	t	p	%	t	p
Dasyurus	CBL							4	-0.6523	0.579	7	-2.575	0.036
hallucatus	APD							8	-0.941	0.433	23	-3.823	0.004
	Sx							13			46	-2.804	0.025
	SMA							7	-1.091	0.361	14	-2.979	0.020
	LCL							9	-1.657	0.296	6	-2.897	0.013
D. viverrinus	CBL	10	-11.885	<0.001	9	-3.429	0.002						
	APD	21	-9.135	<0.001	27	-6.220	<0.001						
	Sx	51	-9.820	<0.001	59	-4.032	<0.001						
	SMA	14	-8.177	<0.001	13	-4.040	<0.001						
	LCL	6	-8.149	<0.001	9	-2.925	0.006						
D.maculatus	CBL	17	-5.776	<0.001	15	-8.028	<0.001	16	-5.068	<0.001			
maculatus	APD	27	-6.236	<0.001	22	-7.081	<0.001	28	-4.009	0.001			
	Sx	53	-4.590	<0.001	67	-6.378	<0.001	69	-4.330	0.001			
	SMA	22	-5.794	<0.001	20	-10.528	<0.001	24	-5.591	<0.001			
	LCL	6	-3.356	0.004	8	-5.587	<0.001	6	-2.669	0.045			
D.maculatus	CBL										12	-1.574	0.223
gracilis	APD										8	-1.512	0.265
	Sx										24	-0.993	0.420
	SMA										15	-1.204	0.320
	LCL										6	-2.285	0.100
Sarcophilus	CBL	9	-7.634	<0.001									
harisii	APD	13	-4.869	<0.001									
	Sx	31	-5.939	<0.001									
	SMA	11	-2.553	0.018									
	LCL	-1	0.316	0.752									
Thylacinus	CBL	20	-7.553	0.003									
cynocephalus	APD	28	-4.450	0.020									
	Sx	86	-4.612	0.007									
	SMA	23	-6.802	0.001									
	LCL	13	-9.683	<0.001									

Table 2.5 Percentage of sexual dimorphism and comparison of means by t-test for. body mass. neck circumference and pes measurements from Cradle Mountain species.

			N	Mean	s.d.	%	t	p
Dasyurus viverrinus	female	mass	27	0.71	0.13	56	-11.610	<0.001
	male	mass	39	1.11	0.15			
	female	neck	7	14.04	1.22	21	-3.767	0.002
	male	neck	9	16.89	1.80			
	female	pes	22	4.81	0.12	8	-9.039	<0.001
	male	pes	35	5.19	0.20			
Dasyurus maculatus	female	mass	10	1.67	0.17	94	-17.821	<0.001
	male	mass	31	3.23	0.39			
	female	neck	5	18.00	1.17	35	-7.257	<0.001
	male	neck	8	24.31	1.96			
	female	pes	9	5.05	0.08	12	-14.690	<0.001
	male	pes	28	5.66	0.17			
Sarcophilus harisii	female	mass	130	5.40	0.96	56	-19.48	<0.001
	male	mass	56	8.43	0.98			
	female	neck	31	29.33	3.38	21	-7.636	<0.001
	male	neck	18	35.47	2.24			
	female	pes	109	6.42	0.19	9	-18.060	<0.001
	male	pes	41	6.98	0.16			

2.3.3 Character Displacement

There is strong evidence for patterning in the form of equal size ratios (non-random distribution) between adjacent morphospecies for canine strength (Sx) among the two quoll species in Tasmania (*Table 2.6, Figure 2.3*). This patterning is apparent when the ratio of the means of adjacent morphospecies are equal to the ratio of the means of the all pairs of morphospecies in the species assemblage under analysis. This patterning, equal size ratios of trophic characters, is evidence of character displacement. Among the dasyurids, the quolls and the devil, patterning occurs in skull length (CBL) but not in Sx (*Table 2.6, Figure 2.4*). There is no evidence of patterning for any character when the analysis is run across all four species of dasyuroids. However, patterning occurs in CBL and Sx when the largest interval is removed. For CBL, this is the interval between male devils and female thylacines. For Sx, the largest interval is between male spotted-tailed quolls and female devils. Devils showed exceptionally high values for canine strength, both sexes exceeding the value for female thylacines and male devils equal in value to male thylacines (*Table 2.6, Figure 2.3*). No other characters, APD, SMA or LCL show patterning in any grouping of the Tasmanian carnivore species, although the result for SMA was almost significant (*Table 2.6, Figures 2.5 - 2.7*). However, LCL showed an interesting result. There were two distinct groups. the two quolls having low values and the devil and thylacine grouped together with high values. Variance within each morphospecies was low for most characters so overlap in variance between morphospecies was only slight .

To test for the effect that differences in face shape between species may have on the results of morphological patterning for the Tasmanian dasyuroids, these analyses were repeated using basi-cranial axis length (BCAL) instead of CBL as a standard measure of body size. No patterning in body size is evident when BCAL is used in any of the species assemblages. This indicates that the patterning in CBL among the Tasmanian quolls and devil is attributable to snout length. Results for the other characters were not altered by the use of BCAL.

The species assemblage of quolls that exists in Tasmania exhibits no patterning when it occurs in the absence of the devil and the thylacine on the south-eastern mainland of Australia. The species assemblages of quolls in south-east Queensland and north-east Queensland, likewise, did not exhibit patterning in any characters. *(Table 2.7, Figure 2.2)*

There is strong evidence for patterning in body mass for the quolls and devil at Cradle Mountain animals. This patterning does not occur when the two quoll species only are analysed. (*Figure 2.8*)

Table 2.6 Barton-David statistics for morphological characters for the quolls (eastern quoll and spotted-tailed quoll, *D. maculatus maculatus*), all of the dasyurids (quolls and the devil) and all of the dasyuroids (quolls, devil and thylacine) in Tasmania. Minimum critical p-value for Bonferroni procedure is 0.01.

Species	Trait	G stat.	G stat. value	nominal prob.	critical p (Rice,1990)	signific.
Quolls	CBL	$G_{1,3}$	0.612	0.052	0.017	
		$G_{1,2}$	0.972	0.019	0.013	
		$G_{2,3}$	0.629	0.354	0.025	
	APD	$G_{1,3}$	0.342	0.219	0.05	
		$G_{1,2}$	0.435	0.464	0.05	
		$G_{2,3}$	0.787	0.192	0.017	
	Sx	$G_{1,3}$	0.969	0.001	0.010	***
		$G_{1,2}$	0.999	0.001	0.010	***
		$G_{2,3}$	0.970	0.025	0.010	
	SMA	$G_{1,3}$	0.677	0.033	0.013	
		$G_{1,2}$	0.727	0.200	0.025	
		$G_{2,3}$	0.931	0.059	0.013	
	LCL	$G_{1,3}$	0.368	0.194	0.025	
		$G_{1,2}$	0.899	0.070	0.017	
		$G_{2,3}$	0.409	0.608	0.050	
quolls and devil	CBL	$G_{1,5}$	0.547	0.004	0.010	***
		$G_{1,4}$	0.571	2.734	0.05	
		$G_{2,5}$	0.612	0.023	0.010	
	APD	$G_{1,5}$	0.166	0.201	0.025	
		$G_{1,4}$	0.339	0.145	0.017	
		$G_{2,5}$	0.166	0.568	0.013	
	Sx	$G_{1,5}$	0.181	0.175	0.017	
		$G_{1,4}$	0.621	0.020	0.010	
		$G_{2,5}$	0.282	1.291	0.050	
	SMA	$G_{1,5}$	0.376	0.029	0.013	
		$G_{1,4}$	0.534	0.038	0.013	
		$G_{2,5}$	0.477	0.733	0.017	
	LCL	$G_{1,5}$	0.004	0.959	0.050	
		$G_{1,4}$	0.019	0.902	0.025	
		$G_{2,5}$	0.078	0.838	0.025	
quolls devil and thylacine	CBL	$G_{1,7}$	0.222	0.036	0.010	
		$G_{1,6}$	0.472	0.007	0.010	***
		$G_{2,7}$	0.248	0.134	0.017	
	APD	$G_{1,7}$	0.139	0.117	0.017	
		$G_{1,6}$	0.284	0.056	0.017	
		$G_{2,7}$	0.166	0.297	0.025	
	Sx	$G_{1,7}$	0.181	0.064	0.013	
		$G_{1,6}$	0.431	0.011	0.013	**
		$G_{2,7}$	0.282	0.092	0.013	
	SMA	$G_{1,7}$	0.071	0.319	0.025	
		$G_{1,6}$	0.096	2.725	0.050	
		$G_{2,7}$	0.376	0.037	0.010	
	LCL	$G_{1,7}$	0.004	0.934	0.050	
		$G_{1,6}$	0.016	0.850	0.025	
		$G_{2,7}$	0.078	0.661	0.050	

Table 2.7 Barton-David statistics for morphological characters for the assemblages of quolls on the south-eastern Australian mainland (eastern quoll and spotted-tailed quoll, *D. maculatus maculatus*), in south-east Queensland (northern quoll and spotted-tailed quoll, *D. maculatus maculatus*) and in north Queensland (northern quoll and northern subspecies of the spotted-tailed quoll, *D. maculatus gracilis*). Minimum critical p-value for Bonferroni procedure is 0.01.

Region	Trait	G stat.	G stat. value	nominal prob.	critical p (Rice,1990)	signific.
s.e. Aust.	CBL	$G_{1,3}$	0.308	1.586	0.050	
		$G_{1,2}$	0.638	0.275	0.050	
		$G_{2,3}$	0.483	0.520	0.025	
	APD	$G_{1,3}$	0.586	0.061	0.010	
		$G_{1,2}$	0.825	0.124	0.017	
		$G_{2,3}$	0.710	0.269	0.010	
	Sx	$G_{1,3}$	0.547	0.077	0.013	
		$G_{1,2}$	0.906	0.065	0.013	
		$G_{2,3}$	0.604	0.382	0.013	
	SMA	$G_{1,3}$	0.372	0.190	0.017	
		$G_{1,2}$	0.646	0.268	0.025	
		$G_{2,3}$	0.577	0.412	0.017	
	LCL	$G_{1,3}$	0.297	0.270	0.025	
		$G_{1,2}$	0.943	0.039	0.010	
		$G_{2,3}$	0.315	0.722	0.050	
s.e. Qld	CBL	$G_{1,3}$	0.121	0.587	0.017	
		$G_{1,2}$	0.266	0.648	0.025	
		$G_{2,3}$	0.457	0.551	0.025	
	APD	$G_{1,3}$	0.242	0.345	0.010	
		$G_{1,2}$	0.287	0.624	0.017	
		$G_{2,3}$	0.844	0.138	0.010	
	Sx	$G_{1,3}$	0.058	0.773	0.050	
		$G_{1,2}$	0.093	0.867	0.050	
		$G_{2,3}$	0.629	0.355	0.017	
	SMA	$G_{1,3}$	0.206	0.405	0.013	
		$G_{1,2}$	0.304	0.604	0.013	
		$G_{2,3}$	0.677	0.303	0.013	
	LCL	$G_{1,3}$	0.094	0.660	0.025	
		$G_{1,2}$	0.615	0.295	0.010	
		$G_{2,3}$	0.153	0.907	0.050	
n.e. Qld	CBL	$G_{1,3}$	0.262	0.130	0.013	
		$G_{1,2}$	0.596	0.311	0.017	
		$G_{2,3}$	0.439	0.572	0.025	
	APD	$G_{1,3}$	0.246	0.339	0.025	
		$G_{1,2}$	0.382	0.519	0.050	
		$G_{2,3}$	0.645	0.337	0.010	
	Sx	$G_{1,3}$	0.333	0.228	0.017	
		$G_{1,2}$	0.576	0.329	0.025	
		$G_{2,3}$	0.579	0.410	0.017	
	SMA	$G_{1,3}$	0.592	0.058	0.010	
		$G_{1,2}$	0.983	0.011	0.010	
		$G_{2,3}$	0.602	0.384	0.013	
	LCL	$G_{1,3}$	0.111	0.613	0.050	
		$G_{1,2}$	0.923	0.053	0.013	
		$G_{2,3}$	0.120	0.937	0.050	

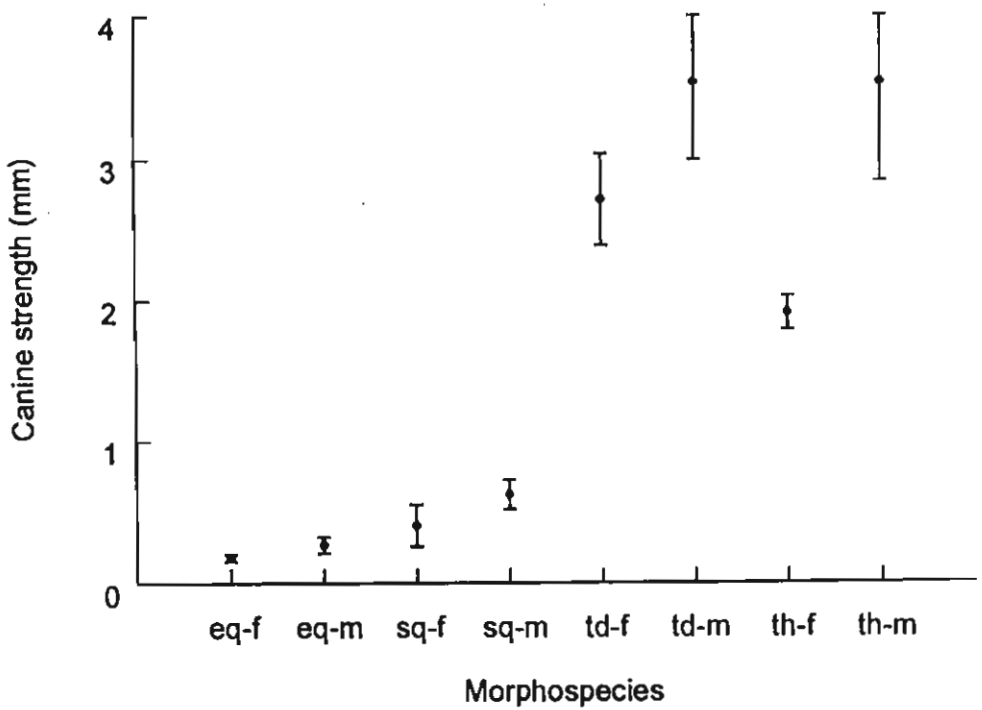


Figure 2.3 Canine strength (Sx) for the four species of dasyuroids in Tasmania. Morphospecies are as follows: f = female, m = male, eq = eastern quoll, sq = spotted-tailed quoll, td = Tasmanian devil and th = thylacine.

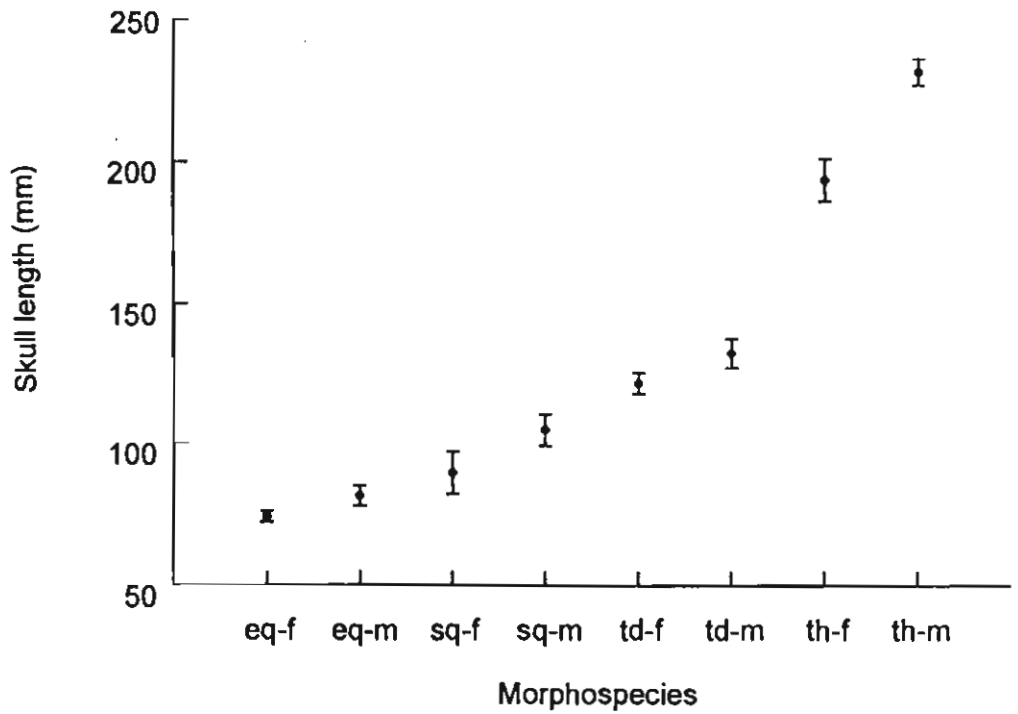


Figure 2.4 Skull length (CBL) for the four species of dasyuroids in Tasmania. Morphospecies as for *Figure 2.3*.

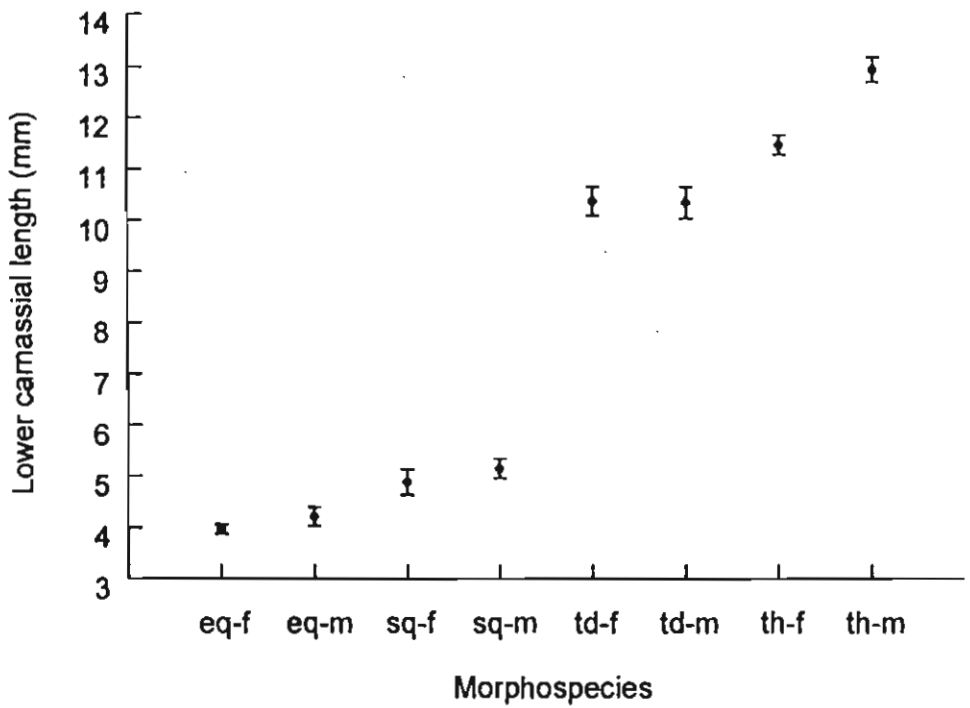


Figure 2.5 Lower carnassial length (LCL) for the four species of dasyuroids in Tasmania. Morphospecies as for *Figure 2.3*.

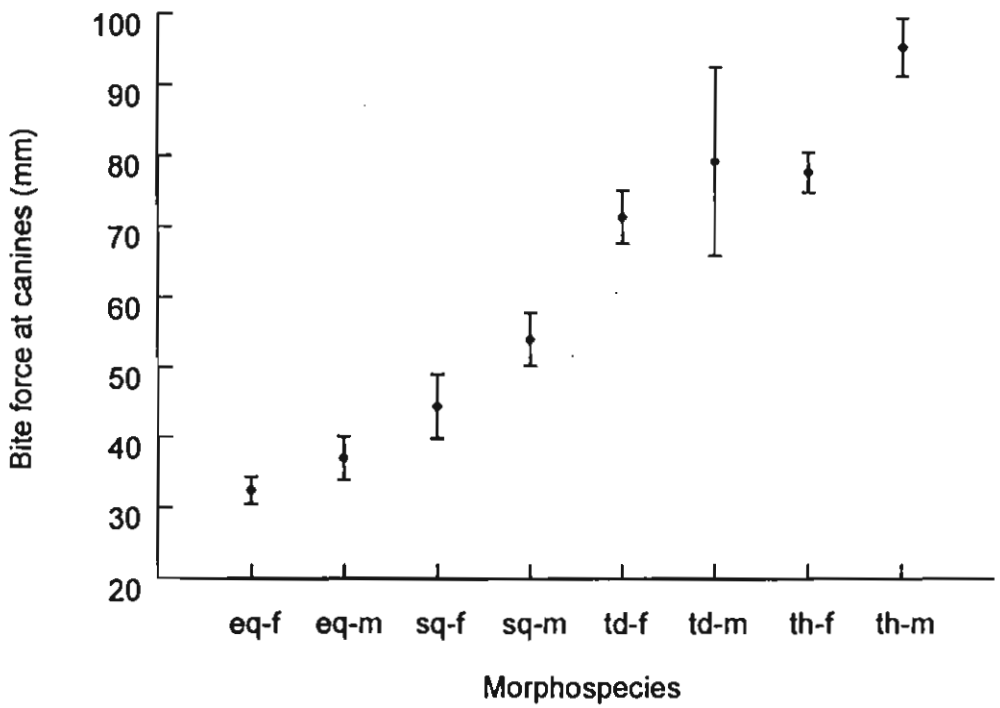


Figure 2.6 Bite force at the canines (SMA) for the four species of dasyuroids in Tasmania. Morphospecies as for *Figure 2.3*.

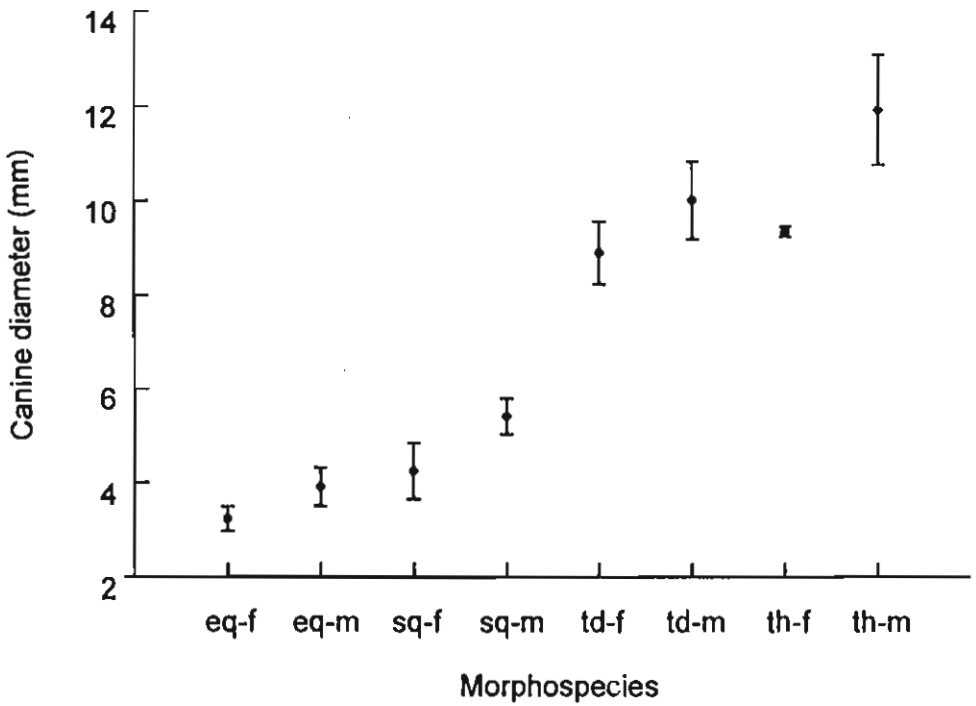


Figure 2.7 Maximal anterior - posterior upper canine diameter (APD) for the four species of dasyuroids in Tasmania. Morphospecies as for *Figure 2.3*.

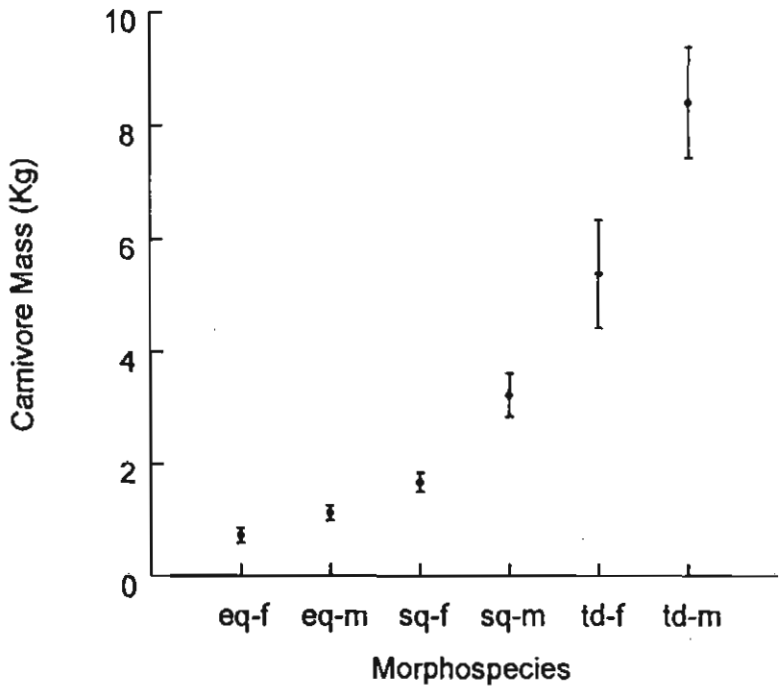


Figure 2.8 Mean body mass (kg) of the three large dasyurid species at Cradle Mountain in Tasmania. Morphospecies as for *Figure 2.3*.

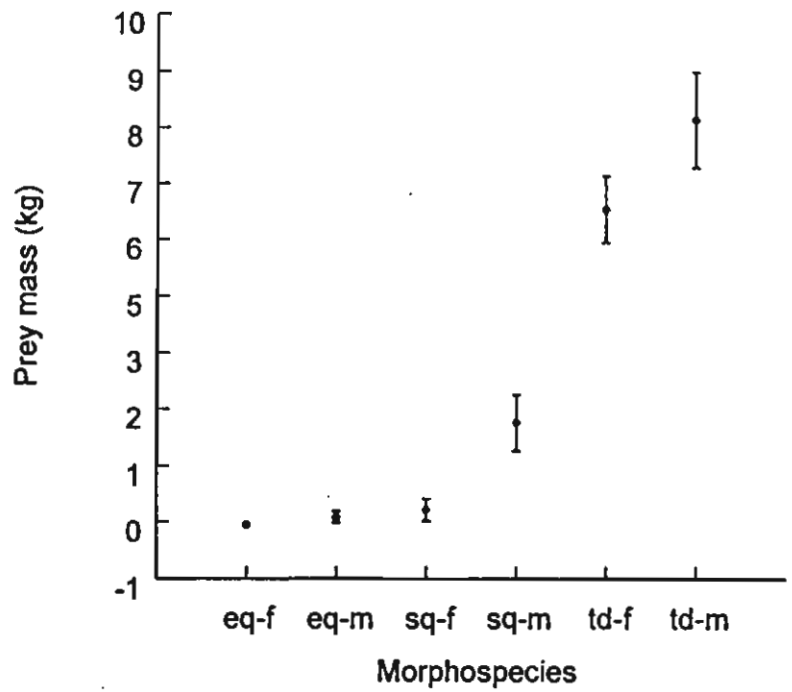


Figure 2.9 Mean prey mass (kg) for the three large dasyurid species at Cradle Mountain in Tasmania. Morphospecies as for *Figure 2.3*.

2.3.4 Prey size

Patterning in prey size for the extant carnivores in Tasmania is demonstrated among the morphospecies of the two quolls (*Dasyurus spp.*), although the result is only just significant at the 0.05% level. Prey size patterning among the two quolls and the devil when analysed as a group is evident only when the smallest interval, that between the male and female devil is removed. (*Table 2.8, Figure 2.9*)

Weighted mean prey masses for each morphospecies, calculated for the Barton-David test, are 42g for female eastern quolls, 154g for male eastern quolls, 394g for female spotted-tailed quolls, 1,832g for male spotted-tailed quolls, 6,222g for female devils and 7,876g for male devils (*Figure 2.9*). Mean prey size increases with body size.

Table 2.8 Barton-David statistics for prey size for the quolls (eastern quoll and spotted-tailed quoll, *D. maculatus maculatus*) and all of the dasyurids (quolls and devil) at Cradle Mountain in Tasmania. Minimum critical p-value is 0.05.

Species	G stat.	G stat. value	nominal prob.	signific.
Quolls	$G_{1,3}$	0.612	0.052	*
	$G_{1,2}$	0.729	0.199	
	$G_{2,3}$	0.840	0.141	
Quolls and devil	$G_{1,5}$	0.153	0.227	
	$G_{1,4}$	0.182	0.367	
	$G_{2,5}$	0.612	0.022	*

2.4 Discussion

2.4.1 Killing behaviour and canine strength

The results of equal size ratios only among the quolls and only for canine strength for the Tasmanian guild of dasyuroids, is consistent with what is known of killing and feeding behaviour in these species. The strong patterning exhibited in canine strength among the quolls reflects the role of the canine teeth in killing behaviour.

Eastern quolls pounce on their prey and inflict initial bites on the thorax. While the prey is pinned to the ground with the fore-limbs, bites are located progressively anteriorly until the killing bite punctures or crushes the skull, or occasionally, severs the spinal cord near its junction with the skull. Once a bite is achieved on the head of the prey, eastern quolls employ a head shake which serves to enhance penetration of the canines and increase the effectiveness of the killing bite. With larger, defensive prey such as rats, quolls aim for the head first. (Pellis & Nelson, 1984; Pellis & Officer, 1987)

Less detailed information is available on the killing behaviour of the spotted-tailed quoll, but they appear to kill in a similar fashion. leaping on their prey and inflicting a killing bite to the head or neck (personal observations; Fleay, 1932). They are well known for killing prey that are large relative to their size (Troughton, 1943; Fleay, 1948; Green & Scarborough, 1990), Jones and Laarn, in prep, Dave Watts, pers.comm., 1992). With large prey such as adult pademelons (*Thylogale billardierii*) three to four times its body size, spotted-tailed quolls leap on the back of the prey, gripping it with all four limbs, a legacy of its arboreal habit (Eisenberg & Leyhausen, 1972). In one instance, the killing bite was positioned with the upper canines in the throat and the lower canines in the back of the neck near the vertebral column. Death was protracted, taking ten minutes and it is unknown whether the cause was spinal damage or strangulation.(Jones and Laarn, in prep.) The extent to which eastern quolls kill prey larger than themselves is unknown but they do kill venomous snakes (Tony Conlan, pers comm., 1992).

The diet of both species of quolls is comprised primarily of mammals, secondarily of birds, with small amounts of reptiles and insects. Reptiles were more important in the diet and a wider range of insects were found in eastern quoll scats than in those of spotted-tailed quolls. Both species of quolls scavenge on carcasses of any size when available although the small size of the prey in relation to the carnivore body size suggests that most prey is killed rather than scavenged. (Chapters 3 and 5)

This dissertation on killing behaviour leads to the point that canine strength can quite sensibly be construed as the most important trophic character involved in prey capture and therefore, in determining the upper limit of prey size that can be handled. It is interesting that patterning showed up in canine strength but not in canine diameter as has been demonstrated for mustelids and felids (Dayan *et al.*, 1989a; 1990). Of all the carnivores, felids and some mustelids have the most specialized killing behaviour. They kill using a nape bite, the canines penetrating the intervertebral space and severing the spinal cord. The canines are well adapted for this purpose, hitting the mark first go in a high percentage of cases, possibly using proprioceptors to guide the bite (Leyhausen, 1979). It is feasible that canine diameter might be adapted to the particular vertebral size and structure of the most frequently encountered prey (Dayan *et al.*, 1989; 1990). Killing behaviour of *Dasyurus spp.* is not as specialised as the felids but neither is it primitive as suggested by Leyhausen, (1979). It consists of a well directed killing bite aimed at the head or neck, perhaps more similar to some of the viverrids (Eisenberg & Leyhausen, 1972). Because death results from crushing of the skull assisted by a head shake to drive the canines in, by crushing of the vertebrae or strangulation, the strength of the canines would appear to be more important than their diameter.

Killing behaviour of devils is different in some respects to the quolls and this is reflected in the lack of patterning of canine strength in the larger dasyurid guild. While they consume a wide range of prey from invertebrates to the largest mammals, large mammals, wallabies and wombats, comprise most of the diet of devils (Chapter 3). Because devils are solitary foragers and are wary of humans, foraging behaviour is rarely seen in the wild, hence little is known of predatory behaviour or the extent to which devils hunt or scavenge. A number of accounts, however, suggest that at

least chasing macropods and wombats is not uncommon (Pemberton, 1990; pers. comm., Joe's uncle Marrawah 1990, Vicki Shilvock 1991, Leon Barmuta 1992, Dave Watts 1993, Klaus Toft 1993). Two recent observations of wild devils at night in the wild suggest that the method for killing large mammals involves gaining a grip with the jaws somewhere on the anterior half of the body, adjusting the bite until a vulnerable area is gained and hanging on with a crushing bite, even being dragged, until the prey succumbs. In one instance, a running devil appeared to chance upon a pademelon behind a shrub. The actual moment of capture was not observed but the devil gained a bite across the forearm and thorax and hung on, without shifting its grip, while it dragged a now feebly hopping pademelon into dense bush. The devil was standing on its hind legs to reach the pademelons chest and death occurred within minutes (Andrew Osborne, pers. comm., 1993). In another instance, a devil was observed running up to an adult wombat, biting it over the snout and engaging in a long tug-of-war. Unfortunately the observer did not stay to see the outcome (Dave Probert, pers. comm., 1993). As is typical of most carnivores, small prey are killed with a well directed bite to the head or neck region (Ewer, 1969).

So very strong canines in devils are consistent with a diet of large prey which are killed by a tenacious crushing bite. Death by crushing, rather than laceration or live consumption as practised by canids and hyaenids (Kruuk, 1972; Dayan *et al.*, 1992), is also consistent with the worn and blunt canines of all but very young devils, and the high values for size of the temporalis muscle (SMA) which relates to force at the canines (*Figure 2.6*). The blunt canines of adult devils would not easily puncture the prey during killing but their strength and the force at the canines produced by massive temporalis muscles would produce a powerful, crushing bite. The possibility of encountering bone which could fracture teeth during the killing bite may also select for strong canines (Van Valkenburgh & Ruff, 1987). *Figures 2.3* and *2.4* demonstrate that the canines of both sexes of devils are much stronger for their body size than either species of quolls or the thylacine.

Thylacines have quite weak canines for their body size (*Figures 2.3* and *2.4*). All that is known of their hunting and killing behaviour comes from anecdotes from bushman, farmers and former hunters. No single detailed report of a hunt exists and it is difficult to distinguish the degree to which reports are constructed from analogies with the wolf. However, the reports generally agree that thylacines leapt out onto prey, perhaps initially crushing it in their jaws, then killed it by eating into the body cavity while pinning it to the ground with their forepaws (Smith, 1982; Guiler, 1985). This killing method bears some resemblance to that of large canids which kill large prey by a series of shallow, slashing bites (Van Valkenburgh & Ruff, 1987). Also similar to large canids, thylacines have narrow, compressed canines, highly suited to producing these sorts of wounds. Bone is unlikely to be encountered during the killing bite hence there is no need for broad canines which can endure mediolateral stresses (Van Valkenburgh & Ruff, 1987). Morphometric analysis suggests that the thylacine functioned more as a fox than a wolf (Werdelin, 1986). My interpretation is that thylacines killed prey smaller than their own body weight, similar to a fox, but that this prey consisted of medium-sized mammals rather than the invertebrate and small mammal prey of the fox because, after all, the thylacine is wolf- not fox-sized (discussed more fully in Chapter 6). This is supported by reports of the diet of the thylacine (Keast, 1982; Guiler, 1985), although Keast does not state

his sources for this information, and by associations of prey species in Pleistocene fossil assemblages and sub-fossil assemblages of prey species associated with Thylacine remains (Case, 1985).

Thus, character displacement for canine strength does not occur across the entire dasyuroid guild, mainly because the devil has so much stronger canines for its body size than the other three species (*Figure 2.3*). This is hardly surprising with such a diversity of killing methods across the four species in the guild.

2.4.2 Competitive Character Displacement

The basis in killing behaviour for the observed equal size ratios in canine strength among the quolls is consistent with the hypothesis of competitive character displacement. This hypothesis is further supported by empirical evidence that the equal size ratios in canines strength result in equal size ratios in prey size and an increase in prey size with body size in the quolls. The effect of the evolution of regular spacing of canine strength, the most important trophic character used in killing prey, between adjacent morphospecies is to create a regularity in the sizes of prey that each morphospecies kills. This reduces competition between these similar, coexisting species and constitutes evolutionary evidence that competition has been an important structuring force in this guild. The lack of patterning in either canine strength or prey size when the devil and the thylacine are included in the analyses indicates that competition is more important between the most closely related species within the guild, the congeners, which have the most similar killing and foraging behaviour.

Size of prey is correlated with body size, both within and between species, among the large dasyuroids in Tasmania (see Chapters 3 and 6). The relationship is not clear-cut, however, which may explain the weak patterning in prey size. Trends of increasing prey size are evident from the smallest morphospecies of the quolls, the female eastern quoll to the largest, the male spotted-tailed quoll. The difference in prey size between the female and male spotted-tailed quoll is much larger than the differences between the other adjacent morphospecies, the female and male eastern quoll, and the male eastern quoll and female spotted-tailed quoll. This relates not to competition for resources, but to the fractal dimensions of the habitat. This is discussed in more detail in Chapter 3, Section 3.4.1.

Although size patterning of canine strength and prey size does not occur when the devil or the thylacine are included in the analyses, prey size is still correlated with body size and even more closely correlated with canine strength in devils and thylacines. Patterning in prey size was evident among the four morphospecies of quolls and the female devil but not when the male devil was included. Type and size of prey items of female and male devils overlap completely for part of the year, so while devils do take larger prey items than spotted-tailed quolls, the lack of regularity in size ratios of canine strength between adjacent morphospecies is reflected in the lack of regularity in prey size (Chapter 3). A critical analysis of the morphology of the thylacine reveals that they probably consumed prey that were of the same size or smaller than the prey of the devil (Chapter 6). This is reflected in the values

for canine strength. Male devils, with a mean body weight of 8.5 kilograms, have canines of a similar strength to male thylacines, which probably had a body weight of around 25 kilograms. Female devils, with a mean weight of 5.4 kilograms, have stronger canines than female thylacines, although female thylacines were larger and probably heavier.

Dayan and Simberloff (1994) provided empirical evidence of predator size / prey size correlations among the mustelids of the British Isles from dietary studies in the literature. Mustelids exhibit equal size ratios in canine diameter, the trophic structure proximal to killing behaviour in these species. Empirical information on diet, necessary for support of the competitive character displacement hypothesis, had been lacking in previous studies of character displacement in mustelids, felids and canids (Dayan *et al.*, 1989a; 1989b; 1990; 1992). Vucetich *et al.* (manuscript) attempted to fill this gap by applying the Barton-David test to prey sizes for some North American mustelids. Unlike this study, however, he did not any find evidence of patterning in prey sizes where morphological patterning among trophic structures occurred. Strong patterning was also exhibited in skull length (CBL) and in body weight among the three species of large dasyurids in Tasmania. This constancy of patterning across several characters is not surprising given the close correlation between measures of animal size (see 2.2.1.1 Methods), but this does not necessarily mean that the characters will depict the same patterns (Dayan *et al.*, 1989). Selection is often assumed to operate on one character such as body size while others are just passively correlated. Lande (1979) provides statistical methodology by which the relative strengths of selection on different characters can be determined. Unfortunately, the data from this study are inadequate for the use of Lande's techniques. Many factors select for body size (Peters, 1983) and since canine strength is likely to relate more directly to diet and thus resource partitioning, it can be assumed that selection is operating primarily on canine strength.

No patterning occurred in basicranial length, the measurement of skull and hence body size that is free of the influence of face shape (Radinsky, 1984), although BCAL is closely correlated with CBL (SL in Radinsky's paper). Length of the snout or rostrum is related to bite strength at the canines (Kleiman & Eisenberg, 1973) so CBL would be more likely to relate to feeding ecology than BCAL. This supports Radinsky's caution that the standard comparison of skull size used should depend on the question being asked. In this study, where differences in the relative sizes of cranial components are being compared across species, BCAL which showed no patterning is the appropriate standard of comparison to use.

No other characters exhibited patterning, although SMA or size of the temporalis muscle, would have shown significant patterning if fewer characters had been examined. This demonstrates why the Bonferroni procedure is employed. SMA is the major muscle group involved in jaw closure and bite strength at the canines and is therefore functionally closely allied with canine strength which was more strongly patterned. The graph of carnassial length (*Figure 2.5*) is interesting for a different reason, to be discussed more fully in Chapter 6. Carnassial length fell into two discreet groups, the small quolls, *Dasyurus sp.*, and the larger carnivores, the devil and the thylacine.

2.4.3 Character release

Character release occurs on the mainland of Australia where the two large species in the Tasmanian guild, the thylacine and the devil, have been extinct for a substantial number of generations. No patterning was found in any characters including canine strength in the quoll assemblage from the south-eastern mainland of Australia. The two species of quolls here are the same species as are found in Tasmania.

No patterning was found either in the other two assemblages of quolls on mainland Australia; south-east Queensland, the region of overlap of the northern limit of the range of the southern subspecies of the spotted-tailed quoll (*D. maculatus maculatus*) and the southern limit of the range of the northern quoll (*D. hallucatus*), and north-east Queensland, where the northern quoll and the northern subspecies of the spotted-tailed quoll (*D. maculatus gracilis*) overlap in distribution. The results for south-east Queensland were expected because while the northern quoll is much smaller than the eastern quoll which it replaces, the spotted-tailed quoll in south-east Queensland is the same size as it is in NSW and Victoria where it overlaps with the eastern quoll. Unfortunately, information on dietary composition and prey size patterning for comparison with Tasmania is lacking from the mainland. The last known eastern quoll population on mainland Australia, in Vaucluse in Sydney, died out in 1966, before systematic studies of diet useful to this analysis were carried out. Similarities are apparent in the diet of the spotted-tailed quoll in prey size range and diversity between Tasmania and Victoria and NSW (pers. comm., Chris Belcher, 1993; Alexander, 1980).

What appears to be happening is that the presence of the two larger carnivores in Tasmania is exerting enough extra pressure on the food resource that the two most similar species in the carnivore assemblage, the congeneric quolls, have evolved morphological patterning in the form of equal size ratios of adjacent morphospecies as a means of reducing competition for food. Morphological patterning may have been exhibited in the mainland quoll guild before the devil and the thylacine became extinct. What we are observing may be character relaxation following competitive release on the mainland. The time scale involved for character displacement or release to occur in quoll teeth is unknown, but evidence suggests that the time scale for character displacement can vary from as little as nine generations to three hundred years to thousands of years in different organisms and situations (Taper & Case, 1992). Thylacines have been extinct on the mainland for not less than 2,000 years. Devils may have been extinct for a similar time in south-eastern Australia or maybe only a few hundred years (Rounsevell, D. and Guiler, E. in Strahan, 1983). The most recent mainland record for the thylacine is 3280+_90 years BP, from Western Australia (Partridge, 1967). A record of 0+-80 years in the Kimberley Region of Western Australia may not relate to the Thylacine bone in the deposit (Case, 1985). The most recent record for the devil in south-eastern Australia is about 5,000 years BP (Gill, 1971), although two records of live animals were recorded in Victoria in 1912. These are commonly thought to be escaped captive devils but there is no certainty of this. Very recent records of devils, 430+/_160 years, come from

Western Australia (Archer & Baynes, 1972). Both species of quolls can breed at twelve months of age, so the minimum generation time is one year. There are possibly 2,000 quoll generations since the thylacine disappeared from the mainland. Even if the devil was extant until very recently, the extinction of just the largest carnivore may have been enough to allow character release to take place.

An alternative hypothesis is that character displacement never occurred on the south-east mainland. The answer to this could be provided by analysis of fossil material of the four marsupial carnivores from this region. The prey base on the mainland is more taxonomically diverse than the impoverished island fauna of Tasmania but the influence of this on the intensity of competition is unknown.

Devils and thylacines were replaced on the mainland by the dingo, the oldest record for which is only 3,450±95 years BP (Gollan, 1984), which is thought to have contributed to their demise. At 10-20 kg, the dingo is intermediate in size between the devil and thylacine. Dingo diet, across a broad geographic area of the forested south-eastern part of Australia, the range of the spotted-tailed quoll and the former range of the eastern quoll, is dominated by larger mammals notably swamp wallabies (*Wallabia bicolor*) (Triggs, Brunner & Cullen, 1984; Robertshaw & Harden, 1986; Brown & Triggs, 1990; Lunney, Triggs & Ashby, 1990). This is similar to the prey type and size of the devil and what is recorded from verbal accounts or cave fauna associations of the thylacines diet (Keast, 1982; Case, 1985; Guiler, 1985).

The question begs as to what impact the dingo had and still has on the mainland quoll species, compared to the devil and thylacine? This is an important question if character displacement used to occur on the mainland. It should be noted that the current survival of the spotted-tailed quoll in many parts of its mainland range seems to be dependent on the presence of dingoes. If dingoes are eliminated, feral foxes move in and spotted-tailed quolls disappear. Inclusion of dingoes in the present analysis would be interesting, but extrapolation would be required to piece together prey size information. Also, the validity of including dingoes in the same guild as the marsupial carnivores is questionable. Although they exploit the same food resource, they do not exploit it in a similar way to the marsupial carnivores. Dingoes, like other canids, are swift, cursorial carnivores with a digitigrade stance that kill their prey by a series of shallow, slashing bites (Dayan *et al.*, 1992). By contrast, the marsupial carnivores are slow moving and not strictly digitigrade, the calcaneum extending to the wrist and heel joints and the animals occasionally resting down on their heels, and they kill using an anteriorly directed crushing bite. Even the thylacine, the most canid-like of the marsupial carnivores and the best-adapted anatomically for cursorial locomotion, is not as specialized for pursuit carnivory as the canids (Keast, 1982) (see Chapter 6). Besides the differences in locomotion and killing behaviour, there are major phylogenetic differences in the dentition between dingoes and marsupial carnivores. The measurement of carnassial length, by which character displacement is expressed in canids (Dayan *et al.*, 1992), is not comparable between canids and marsupial carnivores.

2.4.4 Bergmann's Rule, competitive character displacement and sexual selection

It is interesting that the character displacement observed in the quoll guild is expressed as character convergence rather than the divergence intimated in (Brown & Wilson, 1956) original definition. Theoretical studies using computer modelling indicate that character convergence and even parallel character displacement (both species displaced in the same direction) are as likely to occur as character displacement and all three are consistent with competition theory (Grant, 1972; Abrams, 1986; Vadas, 1990; Taper & Case, 1992). In this study there is a complex interaction of factors selecting for size both within and between species. The two main factors are latitudinal size variation and ecological character displacement. Sexual selection may play an unknown role.

Eastern quolls are larger in Tasmania than on the mainland for all characters, including canine strength and skull length (body size). This increase in body size with latitude is consistent with Bergmann's rule. Latitudinally correlated variables such as temperature and productivity have been claimed to determine body size in some but not all carnivores (Rosenzweig, 1968; Gittleman, 1983). I would expect the same trend with spotted-tailed quolls but, with the exception of King Is., the opposite occurs. Female spotted-tailed quolls were the same size on the mainland as in Tasmania for both skull length and canine strength. Male spotted-tailed quolls, while skull size did not differ, were actually smaller for canine strength in Tasmania. Spotted-tailed quolls from King Island were larger than those from both the mainland and Tasmania. This is consistent with latitudinal size variation and the absence of competition from other predators. Spotted-tailed quolls, now extinct on King Island, were the only mammalian carnivores on the island. The very small sample sizes for King Island, however, preclude confidence in the results.

There seem to be two forces. Bergmann's Rule has influenced an increased body size and canine strength in the eastern quolls in Tasmania. Competitive character displacement, resulting from the increased pressure on the food resource inflicted by the two larger species, the devil and the thylacine, has influenced decreased canine strength in the spotted-tailed quolls in Tasmania. The result is character convergence. This has caused an increase in the prey size overlap among the quolls resulting in increased competition. Morphological patterning in the form of equal size ratios has evolved in response, resulting in a reduction in prey size overlap and hence competition. This combination of size correlated with latitude but mediated by size relationships with congeners, that is, character displacement, has also been demonstrated in congeneric foxes (Dayan *et al.*, 1989).

Sexual selection is the third factor which is probably influencing canine strength, although how this affects the observed morphological patterning is not known. There are two issues to be discussed here.

The first issue is that male quolls and devils of both species have stronger canines than females. Stronger canines in males are tentatively ascribed to sexual selection. In polygynous species such as these, male dominance assessment depends partly on a display of large canine teeth. Although canine strength as opposed to canine size is not directly related to male display, there may be a secondary effect. After all, there

is no point in sacrificing tooth size for sex and starving as a result. No further explanation can be offered at this stage, especially because no patterning was observed in canine size.

Secondly, the degree of sexual dimorphism in canine strength is reduced for both species of quolls in Tasmania compared to the mainland. This effect is greater in the spotted-tailed quolls. On the mainland, spotted-tailed quolls are more dimorphic in canine strength than eastern quolls but in Tasmania, they are equal in the degree of sexual dimorphism. However, reduced sexual dimorphism and reduced size in spotted-tailed quolls in Tasmania occurred only in canine strength and not in body size (skull length) or body robustness. Spotted-tailed quolls at Cradle Mountain still exhibited a greater degree of sexual dimorphism than eastern quolls did in external body features representing robustness, such as neck circumference, a common expression of sexual dimorphism in mammals. Because these species have promiscuous mating systems, where male size and bulk is likely to relate to dominance and access to oestrous females, and because the degree of sexual dimorphism was greater for characters that are related to male dominance than for trophic characters, sexual selection rather than resource partitioning is probably the underlying force driving sexual dimorphism (Shine, 1989). However, the degree of sexual dimorphism in different characters is tempered and could be partially maintained by competitive character displacement (Slatkin, 1984). If competitive character displacement is responsible for the size difference between the two species, then in order for equal size ratios to occur across four morphospecies comprised of two sexes of two species, it is also at least partially responsible for the equal size ratios within the two species. This is supported by weak evidence that the four morphospecies of equally spaced canine strengths are consuming prey of equally spaced mean body mass. This result is consistent with predictions from theoretical models that guilds of sexually dimorphic populations can be produced under certain sets of levels of inter- and intraspecific competition (Vucetich *et al.*, manuscript).

2.5 Conclusions

This study provides evidence of character displacement, with morphological patterning in the form of equal size ratios and character release, consistent with the feeding ecology of marsupial carnivores. The story is not straightforward, however, size relationships result from a complex interaction of latitudinally correlated size variation, competitive character displacement and sexual selection. An alternative hypothesis, that the carnivores have evolved to utilize a prey assemblage that naturally occurs in discreet and equally spaced size categories can be dismissed. The range of prey sizes utilized by all species fall into two size groups (Chapter 3), but within these groups, follow a continuum with, as expected, fewer species at the larger end.

Some caution is desirable in accepting that competition is the force underlying the observed character displacement. Even after a decade of intensive empirical and theoretical research on character displacement, it is still not possible to unequivocally associate the observed morphological patterns with an underlying structuring force such as competition (Simberloff, 1989). The problem is in developing appropriate

null hypotheses to determine this that are themselves free of competition (Abrams, 1986; Simberloff, 1989).

Also, the Barton-David test provides no assessment of variance. Anther statistical test has been published which assess variance as well as the means of characters (MacNally, 1988). There was little or no overlap in the variances of measured characters between adjacent morphospecies in this study, but MacNally's test will be applied to the data to determine if variance affects the test results.

Further research needs to focus on the mechanisms of character displacement. Detailed field research that investigates what happens to each species in allopatry, whether resources are actually limiting, the nature of the resource base, the mechanism of competition and the intra- and interspecific density dependence are required. Theoretical studies suggest that the abundance of the distribution of resources, the growth rates of resources and response of predators, the type and intensity of intra- and interspecific competition and the relative abundances of the predators may be important (Slatkin, 1980; Persson, 1985; Taper & Case, 1985; Abrams, 1986; 1990; Wiens, 1993). I suggest the use of individual-based modelling, a relatively new approach (Judson, 1994), that recognises that community processes occur on a one to one interaction basis between organisms. This approach may assist the theoretical investigation of the sorts of conditions that result in different types of character displacement.

Chapter 3 Diet overlap and relative abundance of sympatric eastern quolls, spotted-tailed quolls and devils

3.1 Introduction

A first step in investigating the importance of competition in structuring guilds is measuring overlap in resource use. With information on resource requirements and resource availability, this may provide indirect evidence for the likelihood of one species affecting another (MacNally, 1983), although a high degree of overlap does not necessarily mean that severe competition is taking place (Wiens, 1977). Competition may result in reduced fecundity, growth or energy stores of individuals and reduced density and/or an altered age structure at a population level (Dunham, 1980 reviewed in MacNally, 1983).

While population densities typically decrease with increasing body size for a broad range of body sizes and taxa drawn from large geographic areas, as explained by the 'energetic equivalence rule' (Blackburn, Harvey & Pagel, 1990; Griffiths, 1992; Cotgreave, 1993), this does not often hold for local communities. Within local communities, the relationship is variable (Griffiths, 1986; Blackburn, Harvey & Pagel, 1990; Cotgreave & Harvey, 1991; Nee *et al.*, 1991; Cotgreave & Harvey, 1992; Cotgreave, 1993). A study of British birds showed a negative relationship between size and abundance on a regional scale, but on the taxonomic scale of tribe the relationship was more likely to be positive, and at the local scale of feeding guilds within communities, the relationship was related to guild type. Only insectivores showed a negative relationship, carnivores and herbivores were more likely to show no relationship and omnivores a positive one (Cotgreave & Harvey, 1991; Nee *et al.*, 1991; Cotgreave, 1993). Brown & Maurer (1986) found a positive relationship for local assemblages of rodents, birds, fish and plants and found that the larger species accounted for more of the energy flow in the local ecosystem. Brown suggested that the ecological advantages of large body size, such as greater energy efficiency, greater mobility and more efficient homeostatic mechanisms enable a greater range of and more favourable habitats to be utilised. Also, large species can dominate resource use. Competitive dominance in interspecific interactions and better avoidance of predators enable more individuals of a larger species to be supported on the same amount of energy than smaller species. These results contradict the 'energetic equivalence rule' which is based on some important and classic studies and suggest that the pattern may be more complex (Brown & Maurer, 1986; Cotgreave, 1993). Cotgreave (1993) concludes that while purely evolutionary phenomena may explain patterns at the highest levels of ecological organisation, at the lower levels such as guilds, purely ecological forces like competitive dominance may provide explanations.

The three species assemblage of marsupial carnivores at Cradle Mountain exhibits high numerical dominance, with a very common and a very rare species. Devils, the largest species, are two and a half times as abundant as the smallest species, the eastern quoll, which is two and a half times as abundant as the middle-sized species, the spotted-tailed quoll. Therefore, devils are five times as abundant as the rare spotted-tailed quoll. Although the largest species is the most abundant, there

is no overall relationship between body size and numerical abundance. Abundance is probably more likely to be affected by competition, particularly since character displacement has been demonstrated in this assemblage. The spotted-tailed quoll is the middle species in body size and overlaps both of the other two species in body weight at some stage of its development (*Figure 3.1*). Independent, young spotted-tailed quolls overlap with adult male eastern quolls during part of their growth and adult male spotted-tailed quolls overlap in weight with young devils for part of the year. It has been demonstrated in numerous species that different age groups as well as sexes can differ in several aspects of feeding ecology, such as prey type and size, foraging location or time of activity (Polis, 1984).

The question of interest in this chapter is whether current interspecific competition is influencing guild structure and causing the disparate relative abundance of the three species, particularly depression of numbers or rarity of spotted-tailed quolls. The hypothesis is that the spotted-tailed quoll is the rarest species because it overlaps in body size, and therefore possibly diet, with both a larger and a smaller species at all stages of its life (all age/sex classes) and therefore experiences greater competitive pressure than the other two species. Both the devil and the eastern quoll overlap in body size with just one other species and only at one part of their life (*Figure 3.1*). Small, young devils overlap in size with adult male spotted-tailed quolls and adult male eastern quolls overlap in size with juvenile spotted-tailed quolls. The available resources of time and manpower on this project precluded the collection of information on resource requirements of the carnivores, availability of prey resources or the experimental manipulations necessary for the demonstration of current competition as the factor causing the observed differences ain abundance. The overall aim of this chapter then is to assess the likelihood that current interspecific competition is influencing population densities of the three species in the assemblage. This will be done by measuring diet overlap, the first stage in the assessment of the importance of competition to guild structure (MacNally, 1983).

The first aim of this chapter is to examine the degree of dietary overlap between the three species when all population classes are combined, between adjacent morphospecies and between age/sex classes where there is an interspecific overlap in body weight.

All three species of large dasyurids at Cradle Mountain are carnivorous, and include a broad spectrum of prey sizes, both vertebrate and invertebrate, in their diet. Mean prey size and therefore prey type is correlated with body size (Chapter 2). Devils consume mostly large and medium-sized mammals such as wallabies and wombats. Spotted-tailed quolls take primarily medium and small mammals, birds and some invertebrates. Eastern quolls eat mainly small mammals and birds and a larger proportion of invertebrates than the two larger species.

Competition is only likely to occur if resources are limiting. Competition theory predicts that in order to coexist, species should diverge in resource use, reducing niche overlap (Wiens, 1993). However, environmental variability means that there may be times of year when food is abundant and times of year when food is scarce. Wiens has labelled these 'fat' and 'lean' times. Accordingly, one would expect niche

overlap to decrease during the lean period when competition is more severe and increase both during the fat time and when food is so scarce that starvation is imminent. However, in a recent review paper, Wiens (1993) states that resource availability alone tells one little about whether the resource availability threshold has been passed. Indeed, species may respond in a three stage sequence of niche overlaps, being opportunistic leading to high overlap when resources are abundant, specialising showing a reduced overlap as resources become limiting, and converging in diet again as resources become extremely scarce and starvation is a prospect.

The second aim of this chapter is to determine whether there is any time of year when environmental stress which may increase energy requirements is high, whether there is evidence of a time of year when animals are more hungry or exhibit physiological or behavioural mechanisms to conserve energy or provide for food shortages, and to determine if diet and diet overlap between species changes with lean and fat times of year. If it does it will indicate the time of year when competition is occurring or is more intense.

The lean time of year was defined as the period in late winter and early spring when the coldest, wettest weather was experienced and when primary productivity would have been at the lowest for the year. At Cradle Mountain over the two and a half years of the field study this occurred between July and October. With continuous rain and frequent sleet and snow, this period was considered to be the most environmentally stressful. At this time of year, prey species in poor condition were seen and dead pademelons (*Thylogale billardierii*) were found. Summers were mild by comparison, being cool with dry periods. The fat time of year was defined as November to March.

A third and minor aim of this chapter is to assess if there is the potential for interspecific competition in any other resources besides food. Fresh water is freely available in this very wet environment but the possibility that suitable dry den sites might be limited was thought to be worth investigating. The degree of overlap in den and den site use was examined.

3.2 Methods

3.2.1 Trapping

Bi-monthly trapping was carried out from November, 1990 to March, 1994. The trapping regime was described in Section 2.2.2.1.

3.2.2 Definition of population classes

Trapped individuals of each species were classified to an age/sex population class.

Young devils were classified as juveniles if they were caught between October and January. October was the earliest date that young of the year were trapped. January was the last month in which the majority of female devils were still lactating. By the next trapping session in March most had regressing mammary glands, meaning that they had weaned their young. Therefore, most of the individuals classified as juveniles were still dependent on their mother for milk. So few young eastern and spotted-tailed quolls were caught between October and January that it was not possible to prescribe accurate weaning dates for these species.

Young of all three species that were trapped from February onwards, and were therefore independent of their mother's milk, that weighed equal to or less than the minimum adult female weight of 5 kg for devils, 1.5 kg for spotted-tailed quolls and 0.5 kg for eastern quolls, were classified as sub-adults (*Figure 3.1*). Individuals reached adult female weight between six and eighteen months later.

Females of all three species were classified as adults if they weighed the same amount or more than the minimum weights stated in the previous paragraph (*Figure 3.1*) or had bred previously (some older females were in poor condition and weighed as little as 4.5 kg). Females reached their final adult weight between one and two years after weaning.

Male devils and eastern quolls were classified as large adults if their body weights were greater than the maximum weight for adult females (*Figure 3.1*). This was above 8.0 kg for devils and above 1.0 kg for eastern quolls. Male spotted-tailed quolls were classified as large adults if they weighed more than 2.6 kg even though the maximum female weight was only 1.9 kg. The higher minimum weight was set for this species because the extreme sexual size dimorphism in body weight (200%) of spotted-tailed quolls means that males smaller than 2.6 kg are still of the light and gracile build typical of females and bear little resemblance to the robust fully-grown male. The large adult male category for all species included some individuals in the final stages of growth.

Males were classified as small adults if their body weight was between the minimum weight for adult females and the minimum weight for adult males. These weight ranges were 5-8 kg for devils, 1.5-2.6 kg for spotted-tailed quolls and 0.5-1.0 kg for eastern quolls (*Figure 3.1*). All males in this category were still growing. Their weights encompassed the range of adult female sizes. This special category of young, growing males based on body size was not created for females. This is considered to be a biologically sound decision because I am interested both in the effects of body size and in the effects of sex . Both males and females reach their final adult weight between twelve and twenty four months after weaning. Most females reach this weight by eighteen months whereas most males take a full two years to complete growth to their comparatively greater final adult weight.

For brevity, throughout this thesis, large adult males are often referred to as adult males or just males, and small adult males are known as just small males.

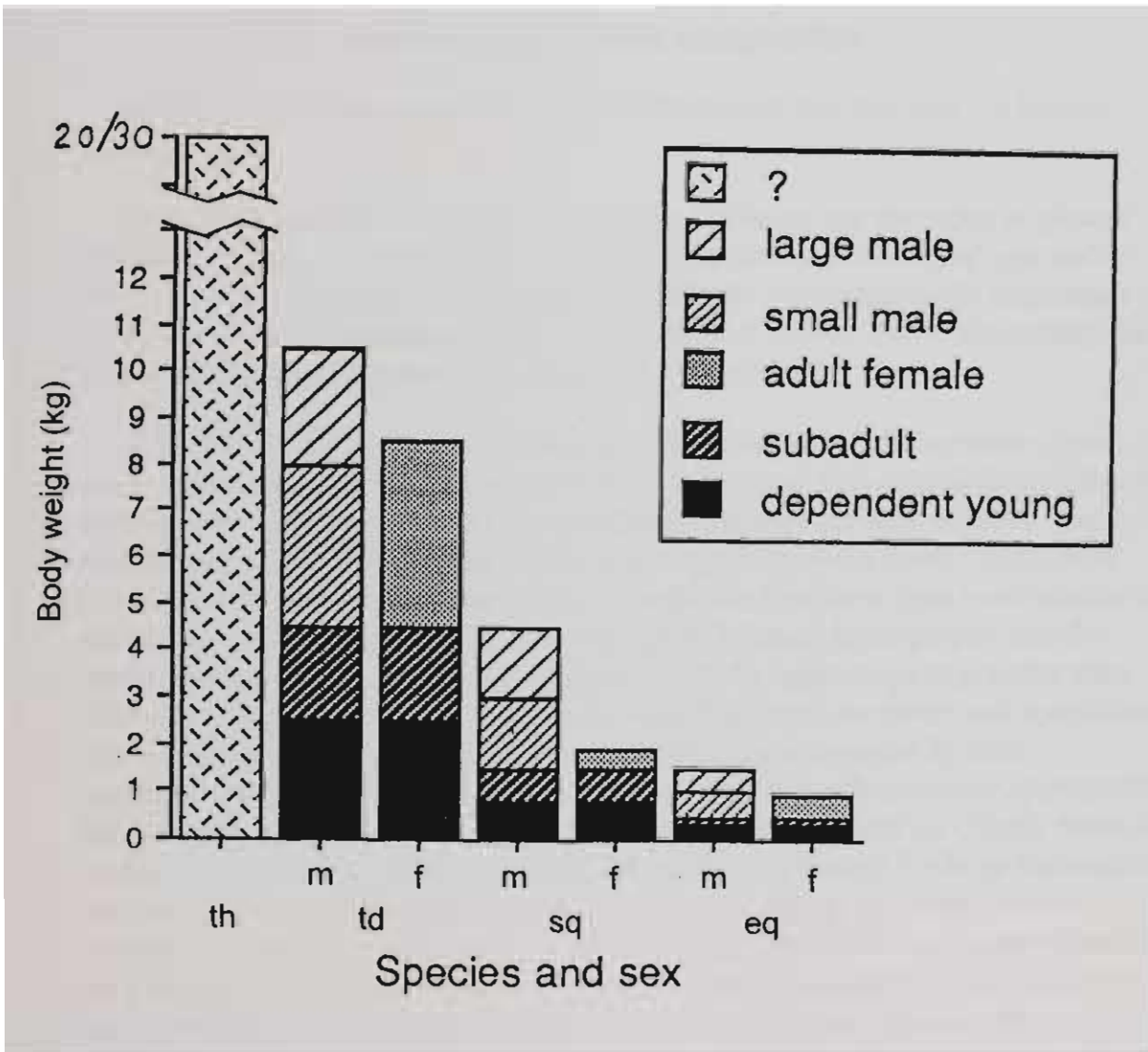


Figure 3.1 Body weights of the age/size/sex population classes of large dasyurids in Tasmania. f = female, m = male, th = thylacine, td = devil, sq = spotted-tailed quoll and eq = eastern quoll.

Definition of critical periods of overlap in body weight for analysis of diet overlap

The period of body weight overlap between sub-adult devils and adult male spotted-tailed quolls, critical for analysis of diet overlap, was defined from February, the month devils are weaned to May for male sub-adult devils and July for female sub-adult devils (which grow more slowly), when they exceed the maximum weight for large, adult male spotted-tailed quolls. The same dates applied to the sub-adult spotted-tailed quoll / large, adult male eastern quoll overlap.

3.2.3 Analysis of diet

3.2.3.1 Determination of diet composition

Methods for identification of prey items from scats was described in Section 2.2.2.2.

Dietary composition data used for analysis of overlap are presented as percent biomass ingested. This takes into account the importance of each prey type and is therefore better than percent occurrence data, which overestimates the importance of small dietary items and underestimates large items (Corbett, 1989). The method used to estimate biomass ingested was developed for this study.

A problem with the method employed in this study is that the number of scats per meal is not known for any of these species. It is assumed that scats defecated in a trap overnight are equivalent in their representation of a meal for each different species and age/size class. Each time an animal was trapped, between 0 and 5 scats were collected. Although the scats were kept separate, the data have been combined as one sample per trap-night. This method of estimating biomass is not precise and the results are to be treated with some caution. Given the large range of predator sizes (700 g to 10 kg) and feeding habits (insectivore/carnivore, carnivore and specialised scavenger), and the large range of prey sizes and types consumed by each morphospecies, I felt that this method was at least as accurate and more appropriate for this study than the methods for estimating biomass proposed by (Floyd, Mech & Jordan, 1978; Corbett, 1989), which rely on conversion factors for large mammalian prey fed to wolves. For example, eastern quolls scavenging on a macropod or wombat do not appear to consume much fur. This would lead to an underestimate in the percentage diet composition for these species as the quantity of fur in a scat is used in the conversion equations. Social dominance may also influence the proportions of bone, fur and flesh consumed by devils (see Chapter 5) thus rendering a conversion factor inaccurate. Conducting feeding trials for each morphospecies for even the most common dietary items was beyond the scope of this study.

The number of each type of prey item in each scat was counted and multiplied by the mean mass for that species (Strahan, 1983; Slater, Slater & Slater, 1989). For the larger mammalian prey species, mass of juveniles was taken as a quarter of adult mass. For prey items larger than 5g, all prey except invertebrates and skinks, a reasonably valid assumption was made that only one individual was present. It was

considered unlikely in this sub-alpine environment that more than one mouse or small bird would be found and eaten in a short period of time. Scavenged human food and plant material could not be quantified.

For skinks and invertebrates other than earthworms, the minimum number of individuals present was estimated from numbers of identifiable parts such as legs and heads. This gives a relatively reliable estimate of the numbers of hard-bodied prey (Dickman & Huang, 1988). For earthworms, the estimate of numbers is not as reliable. Gizzards, often used to count earthworms in scats were not found (Bradbury, 1977). In no case were huge numbers of chaetae found in a scat, and as the hard chitinous chaetae are unlikely to be affected by digestion, the assumption was made that only one earthworm was present per scat. This is a reasonable assumption unless the chaetae that remained behind in the 0.01 mm sieve were only the large gonadal chaetae and the smaller general body chaetae were washed through the sieve. There are only four gonadal chaetae per worm compared to many general body chaetae (Tim Kingston, pers. comm. April 1994). If this is the case, the number of earthworms has been greatly under-estimated. The number and size of chaetae from the earthworm species at Cradle Mountain is under investigation (Tim Kingston).

For prey types larger than an individual of a morphospecies could eat in one meal, an upper limit was placed on the weight consumed. This was set at 40% of body mass for devils, which consume up to this amount in a single meal (Pemberton & Renouf, 1993). A value of 23%, derived from dietary studies based on the sodium turnover technique, was used for eastern quolls (Green & Eberhard, 1983). The value for eastern quolls was also used for spotted-tailed quolls, for which there are no published data, because they are more similar in their feeding habits to eastern quolls than to devils, whose feeding behaviour could be described as gluttony. The mass limits were set at 0.2 kg for female eastern quolls, 0.3 kg for male eastern quolls, 0.4 kg for female spotted-tailed quolls, 0.7 kg for male spotted-tailed quolls, 2.2 kg for female devils and 3.4 kg for male devils. These values are sensible and consistent in relation to feeding observations in the field. In terms of the largest native prey species that were counted as being consumed entirely, these values relate to sugar gliders for both sexes of both species of quolls, adult ringtail possums and juvenile brushtail possums for female devils and adult brushtail possums for male devils.

3.2.3.2 Statistical analyses of diet overlap

As in many field studies of vertebrates, it was not possible to collect independent dietary samples from a large number of different individuals. The same individuals were sampled repeatedly over the study period. Over the two and a half year field period, a total of 19 different individual spotted-tailed quolls, 49 eastern quolls and 126 Tasmanian devils were trapped. With such small numbers of individuals represented in some morphospecies, the chance of a bias occurring as a result of one individual specialising on one particular prey type, is significant. It is not possible to run a test of heterogeneity because of the small number of prey items within any one scat, so a $\chi 2$ test was carried out to see if there are significant differences in the diet composition of individuals within each morphospecies (Kruuk & Moorhouse, 1990). There are no significant differences ($p>0.05$) for any of the morphospecies so all the

data from each individual are used. The exception to this is for adult female devils where, because of the high abundance and trappability of this morphospecies, a large number of samples were collected. One hundred scat records were subsampled, randomly, in order to maximise the number of individuals sampled in each trip. Minimum representative sample sizes for each species were determined after Dickman (1988) using the method of Hurtubia (1973). Dietary records for individuals were incorporated accumulatively until trophic diversity, H_k, stabilised.

Dietary overlap between adjacent morphospecies was calculated using the simple index of resource overlap of Schoener (1968). This index is limited in its usefulness for interpreting similarity of resource use because it does not take into account resource abundance (Hurlbert, 1978). However, it is the most appropriate index to use in this study because conditions required for more sophisticated calculations of diet overlap were not met. For instance, no data were collected on resource abundance and prey species almost certainly varied greatly in abundance.

The Mantel Test was used to provide significance tests for the values of diet overlap between age/sex classes or species (Patterson, 1986; Belbin, 1993). Dietary data based on prey taxa that are used in empirical studies of dietary differences usually violate the assumptions of normal distribution and show too much individual variation to allow a standard contingency table approach (Patterson, 1986). The Mantel Test is a nonparametric test that overcomes the difficulties of using conventional statistical tests. This test calculates the correlation between a matrix containing values for diet overlap between all individuals of two groups (eg. species or sex) and a species identity matrix, then through random permutations where the elements of one matrix are shuffled, constructs a reference distribution and tests whether the correlation between the original matrices is higher or lower than would be expected if there was no difference between the two groups (Fortin & Gurevitch, 1993). A null hypothesis for complete overlap was used, the opposite end of the tail that is usually used in the Mantel test, with the "2) greater than or equal to observed" value in the PATN Analysis Package provided the p-value. The Mantel Test functions as a T-test in that it compares two samples at a time. The Bonferroni procedure was used to correct for the use of multiple comparisons (eg. between five pairs of adjacent morphospecies). Where sample sizes were disparate and a result of no significance was gained, the weighting procedure devised by Luo (1993) was employed.

The Mantel Test is sensitive to small sample sizes (Fortin & Gurevitch, 1993; Luo, 1993) and loses its power to detect differences at sample sizes smaller than ten resulting in Type II errors. Sample sizes of twenty or more are recommended. Another limitation that was encountered in this study is that where there are large numbers of zeros in the matrix the Mantel Test cannot detect differences, even though these differences are apparent in the data. This lack of power arises because the Mantel Test relies on comparing the degree of overlap within groups against the degree of overlap between groups. If within-group overlap is low, the difference between the groups has to be very large (ie. nearly zero overlap) to be detected by the test and return a significant result. Within-group overlap will be low if a large number of individuals scored 100% of biomass in a single prey category, and therefore there are a high proportion of zero overlap values in the diet matrix within a

group. This is a problem in this study with female eastern and spotted-tailed quolls. Very few individuals were trapped and recapture intervals were often long (particularly for spotted-tailed quolls), so most individuals are represented by only one or two scats. With only one or two scats, the likelihood that only one dietary category is found in the scat, and therefore 100% biomass is scored in one food category, is high.

Forty-two categories of prey were found in carnivore scats at Cradle Mountain, including mammals, large birds and crayfish identified to species, small birds and reptiles classified to size groupings, and small invertebrates classified to Order level. These were, in decreasing size order, wombat (*Vombatus ursinus tasmaniensis*), domestic dog (*Canis familiaris*), Bennett's wallaby (*Macropus rufogriseus rufogriseus*), Tasmanian devil (*Sarcophilus harrisii*), Tasmanian pademelon (*Thylogale billardieri*), echidna (*Tachyglossus aculeatus setosus*), spotted-tailed quoll (*Dasyurus maculatus maculatus*), brushtail possum (*Trichosurus vulpecula*), platypus (*Ornithorhynchus anatinus*), ringtail possum (*Pseudocheirus peregrinus viverrinus*), eastern quoll (*Dasyurus viverrinus*), sugar glider (*Petaurus breviceps breviceps*), swamp rat (*Rattus lutreolus velutinus*), long-tailed mouse (*Pseudomys higginsi*), antechinus (*Antechinus swainsonii swainsonii* and *A. minimus minimus* are indistinguishable by hair analysis), white-footed dunnart (*Sminthopsis leucopus leucopus*), house mouse (*Mus musculus*), pygmy possums (*Cercartetus lepidus* or *C. nanus nanus*), Tasmanian native hen (*Gallinula mortierii*), black currawong (*Strepera fuliginosa*), green rosella (*Platycercus caledonicus*), small passerine, bird egg, tiger snake (*Notechis ater*), white-lipped whip snake (*Drysdalia coronoides*), small skink (*Niveoscincus metallicus*), two species of terrestrial crayfish (*Parasticoides tasmanicus* and *Astacopsis tricornus*), earthworm, spider, millipede, moth pupae and larvae (O. Lepidoptera), beetles (O. Coleoptera), grasshoppers (O. Orthoptera), cockroaches (O. Blattodea), dragonflies (O. Odonata), wasps (O. Hymenoptera), flies and larvae (O. Diptera), unidentified large mammal, unidentified small mammal, unidentified bird, unidentified invertebrate. Three further categories, plant material, food scraps and rubbish, could not be quantified by biomass and were excluded from analyses.

Early analyses indicated that with forty-two prey categories, there was so little overlap between individuals within a group (population class/season) being tested, and therefore large numbers of zeros, that differences in degree of overlap between groups could not be detected. This situation arose because, particuarly for the larger morphospecies, there was usually only one prey item per scat. The individual was the unit selected for study and many individuals were only represented by one or two scats. For most of the analyses, the number of prey categories was reduced to ten, as follows: large mammal (wombats to Bennett's wallaby), medium-sized mammal (devil to eastern quoll), small mammal (sugar glider to antechinus), tiny mammal (dunnart to pygmy possum), large bird (native hen to rosella), small bird (all small passerines), snake (tiger and whip), skink, crayfish, small invertebrate (all invertebrates except crayfish).

The rationale for deciding on the size categories of mammalian prey follow that of Holling (1992) who developed a statistical technique to detect the size gaps in assemblages of animals. Working initially with mammal and bird assemblages,

Holling found that animals occur in size clumps with gaps in between where there are no species of intermediate sizes. These size groupings relate to the fractal dimensions of the habitat which in turn relate to a small number of plant, animal and abiotic processes that impose a hierarchy of structure, across a broad range of spatial and temporal scales, on all terrestrial ecosystems. Large and small animals use different dimensions of the same but hierarchically-structured and discontinuous landscape. In structurally complex habitats, there may be several size groupings. The analysis involves an index to detect not clumping but gaps in size between adjacent species. This is devised from the differences in body masses between adjacent species that are arranged in rank order of increasing size (Holling, 1992). Applying Holling's analysis, a significant size gap was detected between my small and medium-sized mammal categories (between sugar gliders and ringtail possums). Two smaller and non-significant gaps occurred between medium and large mammals (pademelon and Bennett's wallaby) and between small and tiny mammals (antechinus and dunnart). Birds were not included in this analysis because they constituted a minor part of the overall diet of the marsupial carnivores at Cradle Mountain. All birds, except currawongs and native hens for which there were few records, are in the small prey size-clump.

To increase the power of the Mantel Test in detecting differences, in a couple of cases mainly involving eastern quolls, where there was still little overlap between individuals within groups, the number of size categories were further reduced to six. These were large mammal, medium mammal, small mammal (small plus tiny), bird (large plus small), other (reptiles and crayfish) and invertebrates. These cases are indicated in the results. The reduction in categories to six made no difference to the results in any of the cases. The sample sizes were too small for the Mantel Test to detect differences.

Where significant differences in diet were demonstrated between seasons, population niche breadth was calculated for each season, following methods used by Dickman (1986b). Because no data were collected on resource availability, only the normalised (B) index (Levins, 1968) was determined.

3.2.4 Demography

Population size of different age/sex classes and species in Cradle Valley at different times was determined as the minimum number of animals known to be alive (MNA), a technique for directly counting the population. MNA is the sum of all individuals trapped over a time period plus all individuals that were trapped both before and after the trapping period although they were not caught during the trapping period (Davis, 1963; Krebs, 1966; Hilbourn, Redfield & Krebs, 1976; Blower, Cook & Bishop, 1981). Only the trappable population is assessed. Pouch young are not included.

Survivorship between seasons was calculated, following the methods of Dickman (1986a), as the percentage of individuals known to be alive in one season that were recorded subsequently.

3.2.5 Seasonal utilisation of carcasses

Seasonal changes in the utilisation of carcasses were detected by three methods. Firstly, an experiment was executed where piles of food were placed at the same locations in Cradle Valley on one night every two months for twelve months and the amount remaining uneaten the next morning was weighed. After preliminary trials, where carcasses of road killed brushtail possums (*Trichosurus vulpecula*) were placed at many locations in Cradle Valley and the number of days elapsed before they completely disappeared was noted, five sites spaced at roughly equal distances along the full length of the study area were selected. Rapid disappearance of carcasses at these sites indicated high carnivore activity. An accurately weighed pile of about 15 kg of carcasses of locally common prey species, mostly brushtail possums, that had been killed on roads, was secured to a tree with wire at each site before dark. The amount of the provided carcasses that was eaten overnight was recorded as one value (sites pooled) for Cradle Valley for every second month. This value was corrected for the biomass of carnivores present in the area in that month. The MNA of each age/sex/species class was multiplied by the mean mass for that class. The amount of provided scavenge eaten was calculated as number of kilogram per kilogram of carnivore present in the study area for that month. Three summer and three winter records of amount of provided scavenge eaten were compared with a student's *t*-test.

Secondly, the frequency and rate at which animals appeared and fed at carcasses that were staked out for observations of feeding behaviour and interactions (Chapter 5) at different times of year and in different weather conditions was summarised.

Thirdly, the species, age and state of decomposition and consumption by carnivores of any naturally occurring carcasses encountered while walking around the study area was recorded in a field journal for the duration of the field study. Where practical, the carcass was monitored to determine for how many days it persisted before it was completely consumed or decomposed.

3.2.6 Body condition

Body condition of each animal was determined for every field trip an individual was trapped using the index devised by Le Cren (1951). This index provides a measure of body condition based on changes in body weight relative to a linear body measurement which does not change with nutritional status. Body condition is only assessed for adult animals because young animals put extra energy into growth rather than body fat. On the first capture for a trip, body weight, head width, hind leg length and pes length were measured on each individual. The linear measurements that best estimate body size for each species were determined in Section 2.2.1.1. They are head width for eastern quolls, pes for spotted-tailed quolls and hind leg for devils.

Following the method of Kruuk, Conroy & Moorhouse (1987) who adapted Le Cren's index for use with otters, mean weight W (in kg) was established as a function

of mean length L (in cm) for each sex of each species, for both pes and the best measure of body size for each species (ie. head width, pes or hind leg), :

$$W = a.L^n$$

The values for the constants *a* and *n* are as follows:

for 9 female eastern quolls -	for pes a=0.015 and n=2.448
	for head width a=0.006 and n=3.391
for 39 male eastern quolls -	for pes a=0.028 and n=2.156
	for head width a=0.01 and n=3.034
for 5 female spotted-tailed quolls -	for pes a=0.006 and n=3.532
	for 10 male spotted-tailed quolls - a=0.004 and n=3.797
for 43 female devils -	for pes a=0.363 and n=1.44
	for hind leg a=0.004 and n=2.921
for 27 male devils -	for pes a=0.103 and n=2.203
	for hind leg a=0.001 and n=3.337.

An index of body condition *K* was calculated for each trip for each individual following the method devised by Le Cren (1951) in his study of body condition of fish:

$$K = W/(a.L^n)$$

Seasonal differences in body condition were detected by one-way analysis of variance across six bi-monthly periods. Tukey Honest Significant Difference was used to determine where the differences are.

3.2.7 Food caching

In June, 1992, the fate of six carcasses of road killed brushtail possums were followed in an area that had been saturated with food for two nights. 10.2 kg of possums had been consumed there the previous night from a pile of 15 kg of possums set out for the experiment on seasonal utilisation of carcasses, and a 9 kg Bennett's wallaby (*Macropus rufogriseus bennetti*), staked out to observe feeding interactions, had been consumed by devils between 17:00 hours and 21:30 hours. At 23:00 hours, six possum carcasses were left on the ground unsecured, each with a 240 m spool and line tracking device glued to the base of the tail (see Chapter 4 for details of construction of spools and application of the technique). The next morning each of the spools was followed until the end or the carcass was reached and details of the remains, distance moved, type and density of habitat where it was consumed and the situation of any remains was recorded. Any attempt to hide in dense bush, cover or bury food is evidence that food caching is used as a method of storing surplus food for future use.

3.2.8 Body temperature and winter activity

See attached manuscript. Jones, M.E., Grigg, G. and Beard, L. Body temperatures and activity of Tasmanian devils (*Sarcophilus harrisii*) and eastern quolls (*Dasyurus viverrinus*) through an alpine winter. (Jones, Grigg & Beard, manuscript)

3.2.9 Dens

For any carnivore dens that were found at Cradle Mountain the following information was recorded; the height and width of the entrance tunnels, habitat type, slope, distance to the forest verge, and a general description of the den. Dens were usually discovered while radio-tracking or spool-and-line tracking.

3.3 Results

3.3.1 Overlap in diet, overlap in body weight and relative abundance of adjacent species

3.3.1.1 Overlap in diet between adjacent species and morphospecies

Minimum representative sample sizes

Accumulated trophic diversity stabilised for devils after fourteen individuals were analysed. The results for both species of quolls were inconclusive. Diversity did not increase at all, remaining stable from the first record (a record is the diet composition of accumulated scats for one individual), although there was a fluctuation in the middle of the graph for eastern quolls. This fluctuation was caused by one record that had a very large number of one type of dietary category, namely insects. The implications for analysis of the diet of quolls are that large numbers of scats are needed from each individual. In this study, very few female quolls were caught (dietary information was available on only six of each species) and many of these were only caught once. The problems this presented for analysis are discussed throughout the dietary results.

Between species

When the data from large adult males, adult females and small adult males are combined for each species, diet of each of the three species of marsupial carnivores at Cradle Mountain is significantly different from the other two species. The largest differences are between eastern quolls and devils, and between eastern quolls and spotted-tailed quolls (Mantel Test, both p=0.001, both detected when analysed with ten prey categories). Detection of the difference between spotted-tailed quolls and devils required further reduction of prey categories to six (see section 3.2.3.2) and the

difference is only just significant (Mantel Test, p=0.02: critical p value using Bonferroni procedure is 0.02) (*Table 3.1*). As is revealed in subsequent analyses, the diets of male and female spotted-tailed quolls are different, with that of male spotted-tailed quolls being quite similar to female devils. There are a large number of records for males and very few for females. In this analysis, where diet of males and females are combined, the disproportionately large number of male records is skewing the mean prey type towards the larger species that comprise the bulk of the devils diet, introducing a level of artefact in the results of the analysis.

Devils are carnivores feeding primarily on large mammals, secondarily on medium-sized mammals. Small mammals and birds are of minor importance. In the diet of spotted-tailed quolls, medium-sized mammals are the most important, followed closely by large mammals then small mammals and birds. Some invertebrates are eaten. Female spotted-tailed quolls feed primarily on the smaller prey species. With more gender equitable sample sizes, small mammals and birds would have a greater representation in the overall diet for this species. Eastern quoll diet is more diverse than the other two species, with a representation of at least three percent in all prey categories. Medium-sized, small and tiny mammals, large and small birds, skinks and small invertebrates (including insects, spiders and earthworms) are eaten in fairly equal proportions by mass. Large mammals, snakes and crayfish are also consumed in reasonable quantities. (*Table 3.1*)

Of the items that cannot be quantified, the scats of all three species contain scavenged food scraps and rubbish, and ingested plant material. Eastern quolls consume more plant material than the other species. However, it is not finely macerated and is mostly grass. As these animals forage for cryptic grass-dwelling creatures, ingestion of this grass may be incidental. (*Table 3.1*)

Table 3.1 Diet of the three species of marsupial carnivores

Percentage biomass	Devil (%)	spotted-tailed quoll (%)	eastern quoll (%)
large mammal	61	28	4
medium mammal	37	33	15
small mammal	<1	17	15
tiny mammal	0	3	11
large bird	1	7	8
small bird	<1	11	16
snake	0	0	4
skink	0	<1	13
crayfish	0	<1	3
small invertebrate	0	0	11
plant (% occurrence)	3	3	55
food scraps (")	15	20	7
rubbish (")	12	21	20
No. individuals	54	19	51

Statistical significance: Mantel Test
(critical minimum p value (Bonferroni) = 0.02)
devil: spotted-tailed quoll, p=0.02
devil: eastern quoll, p=0.001
spotted-tailed quoll:eastern quoll, p=0.001

Between morphospecies

Although a slightly larger percentage of the diet of adult male devils is made up of large mammals than of medium-sized mammals, compared to the diet of adult female devils, there is no statistical difference in the diet of the sexes (Mantel Test, p=0.54). Small adult males of the same body weight range as females, do not differ significantly in diet to either adult males or females. Their diet is more similar to females than males (Mantel Test, male p=0.28, female p=0.69). (*Table 3.2*)

A greater difference is apparent between the diets of female devils and male spotted-tailed quolls, although it is still not significantly different (Mantel Test, p=0.14). The diet of female devils comprises a higher percentage of large mammals and that of male spotted-tailed quolls comprises more small mammals and birds. (*Table 3.2*)

The only comparison of diet overlap between adjacent morphospecies which produces results approaching significance is the difference between male and female spotted-tailed quolls (Mantel Test, p=0.02). Despite the small sample size for females, the difference visible in the data is so marked that it was almost detected by the Mantel Test, suggesting that a Type II error has occurred. Note that the rather conservative Bonferroni procedure (discussed in Chapter 2, Section 2.2.1.3) sets the minimum critical p value at 0.01, rendering this result not significantly different. Larger sample sizes for females, at least greater than ten individuals, are required. With larger sample sizes, the apparent differences would probably be significant. (see discussion in Methods section 3.2.3.2)

No significant differences in diet are detected between female spotted-tailed quolls and male eastern quolls (Mantel Test, p=0.25) although differences are apparent in the data. Female spotted-tailed quolls eat greater quantities of larger mammals and birds, and fewer reptiles and invertebrates than male eastern quolls. Little confidence should be placed in the statistical results for this analysis because the sample size for female spotted-tailed quolls is very small resulting in a high Type II error rate. With larger sample sizes, the apparent differences may be statistically significant.

No trends of a body size / prey size relationship can be seen in the data in the comparison between male and female eastern quolls and no significant difference was found (Mantel Test, p=0.12) (*Table 3.2*). Sample sizes for females are very small however (n=6). No differences are found either, between large and small adult male eastern quolls where sample sizes are quite respectable (22 and 23, respectively) (Mantel Test, p=0.64) or between small male and adult female eastern quolls (Mantel test, p=0.61). It is difficult to confidently say anything about differences between the sexes of eastern quoll. Sample sizes for females are so small that differences cannot be detected with the Mantel Test. There is also the problem that derives from high variability in diet between scats and individuals for all individuals that may be obscuring real differences in the data. (see discussion in Methods section 3.2.3.2)

Table 3.2 Diet of the morphospecies of marsupial carnivores

Percentage biomass	adult male devil (%)	adult female devil (%)	small male devil (%)	adult male spotted-tailed quoll (%)	adult female spotted-tailed quoll (%)	adult male eastern quoll (%)	adult female eastern quoll (%)	small male eastern quoll (%)
large mammal	67	59	55	34	16	5	0	0
medium mammal	31	39	45	42	15	12	15	16
small mammal	<1	<1	<1	10	29	10	31	22
tiny mammal	0	0	0	4	2	13	<1	0
large bird	2	<1	<1	3	15	6	14	3
small bird	0	<1	0	7	22	15	19	12
snake	0	0	0	0	0	9	2	5
skink	0	0	0	0	0	16	1	24
crayfish	0	0	0	0	1	4	<1	4
small invertebrate	0	0	0	0	0	10	17	14
No. individuals	18	36	13	11	5	22	6	23

Statistical significance: Mantel Test (critical minimum p value (Bonferroni)= 0.01)

male devil: female devil, p=0.54
female devil: male spotted-tailed quoll, p=0.14
male spotted-tailed quoll: female spotted-tailed quoll, p=0.02
female spotted-tailed quoll: male eastern quoll, p=0.25
male eastern quoll: female eastern quoll, p=0.12
small male devil: adult male devil, p=0.28
small male devil: adult female devil, p=0.69
small male eastern quoll: adult male eastern quoll, p=0.64
small male eastern quoll: adult female eastern quoll, p=0.61

3.3.1.2 Overall relative abundance

The total number of each species, calculated as the minimum number of animals known to be alive (MNA), over the entire field study period is summarised in *Table 3.3*. Devils are two and a half times more abundant than eastern quolls and six times more abundant than spotted-tailed quolls. Eastern quolls are two and a half times more abundant than spotted-tailed quolls. Even if the same number of female quolls of both species had been caught as males, these proportions would not change much. An increased capture rate of female quolls with pouch young or when lactating and the paucity of captures at other times of year suggest that the disparate sex ratio is an artefact resulting from trap shyness of female quolls.

Table 3.3 Total number of individuals (MNA) of each species at Cradle Mountain over the entire study period from November 1990 to March 1993.

	male	female	total
devil	58	68	126
spotted-tailed quoll	12	7	19
eastern quoll	40	9	49

3.3.1.3 Overlap in body weight between adjacent species

Body mass of age/sex classes for each species is summarised in *Table 3.4*. Note the almost complete overlap in body weight between sub-adult devils and adult male spotted-tailed quolls, and between sub-adult spotted-tailed quolls and adult male eastern quolls for the first 4-6 months after weaning of juveniles in February. Also note the overlap in body weight between juvenile devils between October and January and adult female spotted-tailed quolls. No juvenile spotted-tailed quolls were captured so a similar comparison with eastern quolls cannot be made.

Table 3.4 Body mass of age/sex classes for all three species

Species	Age/sex class	Month	N	Mean (kg)	Range (kg)	S.D.
devil	adult male	-	56	8.43	5.0-10.4	0.98
	adult female	-	138	5.40	3.6-8.5	0.96
	subadult	male: Feb.-May female: Feb.-Jul.	92	3.04	1.7-4.8	0.80
	juvenile	Oct.-Jan.	22	2.26	1.2-3.3	0.58
spotted-tailed quoll	adult male	-	31	3.23	2.6-4.2	0.39
	adult female	-	10	1.67	1.4-1.9	0.17
	subadult	as above for devils	5	1.21	0.95-1.5	0.21
eastern quoll	adult male	-	38	1.12	0.95-1.5	0.14
	adult female	-	28	0.71	0.5-0.95	0.12
	subadult	as above	4	0.45	0.4-0.5	0.04

3.3.1.4 Overlap in diet during annual period of overlap in body weight between species

Diet overlaps significantly between adult male spotted-tailed quolls and sub-adult devils (Mantel Test, p=0.29), and between sub-adult devils and adult devils (Mantel Test, p=0.22) during the months of the year when body weight overlaps. Differences in the diet between sub-adult devils and large adult male spotted-tailed quolls are apparent in the data though. The diet of sub-adult devils is intermediate between that of adult male spotted-tailed quolls and adult devils. Birds constitute a substantial percentage of the biomass of the diet of both sub-adult devils and adult male spotted-tailed quolls but rarely appear in the diet of adult devils. Also, large mammals constitute a higher percentage of the diet of sub-adult devils than of the diet of adult male spotted-tailed quolls, although the proportion for sub-adult devils is still less than that for adult devils. (*Table 3.5*). Only the difference between adult devils and adult male spotted-tailed quolls is significant however (Mantel Test, p=0.001). (Critical p value for these tests, using the Bonferroni procedure, is 0.016.)

Table 3.5 Diet overlap of adult and sub-adult devils and adult male spotted-tailed quolls during the period of body weight overlap between February and July. The number of unidentified prey items was negligible.

Percentage biomass	adult devil (%)	sub-adult devil (%)	adult male spotted-tailed quolls (%)
large mammal	49	33	4
medium mammal	47	47	77
small mammal	2	7	4
tiny mammal	1	0	<1
large bird	1	1	14
small bird	<1	12	1
snake	0	0	0
skink	0	0	<1
crayfish	0	0	0
small invertebrate	0	0	0
No. individuals	42	45	6

Statistical significance: Mantel Test (critical minimum p value (Bonferroni) = 0.016)
sub-adult devil: spotted-tailed quoll, p=0.29
sub-adult devil: adult devil, p=0.22
spotted-tailed quoll: adult devil, p=0.001

Juvenile devils, the age class smaller and younger than sub-adult devils, overlap in body weight with the smaller population classes of spotted-tailed quolls (small adult males, females and sub-adults). However, the diet of juveniles devils is very different from that of small spotted-tailed quolls (Mantel Test, p=0.001) (*Table 3.6*). The diet of juvenile devils overlaps substantially with that of the larger sub-adult devils (Mantel Test, p=0.56), adult male spotted-tailed quolls which are the same body weight as sub-adult devils (Mantel Test, p=0.77) and adult females at the same time of year, their mothers, (Mantel Test, p=0.42). The critical p value for these four comparisons is 0.013 (Bonferroni procedure).

The diet of juvenile devils is intermediate between that of the three larger morphospecies in this comparison, with all of which it overlaps substantially (*Table 3.6*). The diet of juvenile devils also shares some features of the diet of the similar sized morphospecies, the female spotted-tailed quoll and the male eastern quoll. Medium-sized mammals are more important in the diet of juvenile and sub-adult devils than in the diet of adult female devils, where large mammals constitute a higher percentage of the biomass. Larger prey species constitute a greater proportion of the diet of juvenile devils than of adult male spotted-tailed quolls, even though the latter are larger in body size than the juvenile devils. Birds constitute a substantial percentage of the biomass of the diet of both juvenile and sub-adult devils, male and female spotted-tailed quolls, but are rarely recorded in the diet of adult devils. Snakes are found in the diet of juvenile devils. The only other morphospecies in which snakes are found in the diet are eastern quolls (*Table 3.2*).

There are insufficient data to analyse diet overlap between sub-adult spotted-tailed quolls and adult male eastern quolls during the months of body weight overlap.

Table 3.6 Diet overlap of juvenile devils from October to January with adult female devils (Oct.-Jan.), sub-adult devils (Feb.-May/July) and with all small (small male, female, sub-adult) spotted-tailed quolls (data for whole year used).

Percentage biomass	female devil (%)	sub-adult devil (%)	juvenile devil (%)	male spotted-tailed quolls (%)	all small spotted-tailed quolls (%)
large mammal	54	33	38	28	16
medium mammal	44	47	46	33	17
small mammal	1	7	5	16	45
tiny mammal	0	0	1	3	3
large bird	<1	<1	2	7	<1
small bird	<1	12	5	11	10
snake	0	0	3	0	0
skink	0	0	1	1	<1
crayfish	0	0	0	1	<1
small invertebrate	0	0	0	0	8
No. individuals	20	45	18	11	13

Statistical significance: Mantel Test (critical minimum p value (Bonferroni) = 0.013)

female devil: juvenile devil, p=0.42
sub-adult devil: juvenile devil, p=0.56
juvenile devil: male spotted-tailed quolls, p=0.77
juvenile devil: small spotted-tailed quolls, p=0.001

3.3.1.5 Relative abundance during annual period of overlap in body weight between species

Table 3.7 sets out the number of individuals in different species/sex/age classes which overlap in weight with other such classes. It demonstrates the large number of sub-adult devils (mean = 25) in the population at Cradle Mountain that overlap in body weight, between February and May (for males) or July (for females), with a small number of adult male spotted-tailed quolls (mean = 4). For the remainder of the year, there is no body weight overlap between devils and spotted-tailed quolls. *Table 3.7* also demonstrates the larger number of adult male eastern quolls (mean = 9) during this period of body weight overlap that coexist with very few sub-adult spotted-tailed quolls (mean = 2).

Dependent juveniles of the year of all three species are first trapped when they begin to range away from the den in October. Numbers of dependent juveniles are under-represented because they are rarely caught. Capture rates increase as the juveniles grow, reaching a maximum in March when all young of the year are weaned.

Table 3.7 Relative abundance (MNA) of different population classes of all three species during the period of weight overlap (Feb.-May/July) and during the remainder of the year. * these sub-adults are now larger than the adult male of the next smaller species

	adult male	small male	adult female	sub-adult	juvenile	total
Feb.-May/Jul.						
devil	7	3	18	25	0	53
spotted-tailed quoll	4	1	2	2	0	9
eastern quoll	9	9	5	1	0	24
Jul./Sept.-Jan.						
devil	5	5	15	*10	11	46
spotted-tailed quoll	4	1	1	*1	0	7
eastern quoll	3	6	1	0	0	10

3.3.2 Is there evidence of seasonal food stress or of changes in diet and diet overlap between seasons?

3.3.2.1 Evidence of seasonal food stress

Carcass disappearance

The carcass disappearance experiment produced a result of no significant difference in the amount of scavenge consumed per biomass of carnivore between winter (mean=0.18, *sd.*=0.08) and summer (mean=0.17, *sd.*=0.12) (t= 0.04, df=3.6, p=0.97). There is large variability in the weight of carcasses that are consumed by carnivores in one night in Cradle Valley in both seasons, and no trends are visible. Many more than three data points per season would be required to detect differences. The raw data are presented in *Table 3.8*.

Table 3.8 Kilograms of carcasses, of locally common prey species, consumed per kilogram of carnivore (MNA) at Cradle Mountain on six nights over a twelve month period.

Date	Season	kg carcass consumed / kg carnivore
Jun., '92	winter	0.15
Aug., '92	winter	0.11
Oct., '92	winter	0.27
Dec., '92	summer	0.12
Feb., '92	summer	0.09
Apr., '92	summer	0.31

Carcasses and remains of carcasses were found at all times of year at Cradle Mountain. They included birds, brushtail possums, pademelons and wombats. The

only dead animals whose death could confidently be attributed to environmental stress were three pademelons found in September and November towards the end of a prolonged period of snow cover and cold, wet weather. One of these was in the middle of a large patch of rainforest, but the other two carcasses were in open grassland where feeding experiments were regularly carried out and carcasses usually disappeared in one to two nights (see Chapter 5). These two carcasses, present at the environmentally most stressful time of year for all wildlife including the carnivores, were only nibbled on even one week after they died. Although this was only one incident the implication is that the devils that came to feed on these carcasses were not overly hungry.

No carnivore turned up to feed on seven out of eighteen periods of observation (each one or two nights, totalling twenty nine nights) of feeding behaviour at carcasses. On three occasions, one devil arrived but left after only nibbling at the carcass. On two of these three occasions, the devil left when snow started to fall. One of these cases involved the largest male devil known at Cradle Mountain (weight of 10.5 kg), tattoo #58. He had been observed chasing a pademelon four kilometres away forty-five minutes before turning up at a 30 kg wombat carcass staked out for feeding observations. He attempted to drag the carcass (which was wired to a tree) into dense bush, then rolled it over a few times, bit off one foot, swallowed it and departed. This was in June, very cold and wet, with snow on the ground. On two of the occasions when no animal turned up, there was snow on the ground or snow was impending. However, in the five remaining cases, one in which a carnivore showed up only briefly and four where no animals turned up at all, the weather was not severe. My impression, based on this limited number of observations, is that devils were no more hungry or inclined to find or feed on a carcass in late winter, the environmentally most stressful time of year, than at any other time.

In conclusion, there seemed to be no indication of seasonal food stress, as detected by animals consuming carcasses in larger quantities or faster in winter. If anything, carcasses were left uneaten more frequently in periods of severe winter weather.

Survivorship

Loss of a substantial amount of body condition or high mortality towards the end of winter is also indicative of seasonal food stress. A build up of fat reserves in summer to tide over the winter can also be considered as an adaptation to seasonal shortcomings in energy requirements, so body condition is addressed in the next section. Seasonal trends in mortality can be addressed by examining relative abundance and survivorship in both the lean (environmentally stressful) and fat times of year.

Survivorship is higher in the lean time of year (environmentally stressful period from late winter to early spring, July to October) than in the fat time (the remainder of the year) for all population classes and species for both years (*Table 3.10*). However, relative abundance for the equivalent period (*Table 3.9*), shows that there are more individuals of all three species present in the study area from November to June than there are from July to October. This is because the resident animals do not range widely in late winter/early spring, as evidenced from trapping records. From

August to December, females of all species that have bred are closely bound to the vicinity of a den site containing young (Pemberton, 1990). Once young are weaned, trapping records indicate that at least female devils range much more widely until the following July when they again leave young in a den. The fat time of year also covers the mating period for all three species (late February to early April for devils, May to June for both quoll species) when males are expected to range widely. Very few adult male or female devils are trapped in March. Rather than high survivorship in the lean season representing low mortality at this time of year, I suggest it means a high degree of residency and low mobility. The low survivorship in the fat season represents the large proportion of transient animals that are not year-round residents of the study area and may not be trapped more than once. The lower survivorship of sub-adults than adults in late summer probably represents a genuinely higher mortality of newly weaned young animals.

Another trend that needs explanation is the decline in numbers of devils and eastern quolls in the study area over the duration of the study. The dead-ended access road, which runs the full length of the longitudinally-shaped study area, was upgraded as far as the National Park boundary, one third of the distance into the study area, in June 1991, ten months after the study was commenced. The eastern quoll population declined rapidly from nineteen to a single individual by July 1992 and remained at this level for much of the rest of the study. Seven carcasses of eastern quolls collected from the road indicated that road mortality was a primary factor. Devils also appeared to be significantly affected with their somewhat larger initial population declining at the same rate. Twelve devils were also found dead on the road, out of an initial population of 39. No carcasses of spotted-tailed quolls were found (Jones, 1993). Steps are currently being taken to reduce mortality of wildlife on this road.

Table 3.9 Relative abundance (MNA) of population classes of the three species of carnivores at Cradle Mountain at the lean (July - October) and fat (November - January) times of year for Nov. 1990 to Oct. 1992. The last few months of information are not used because of limitations of the MNA technique.

	adult male	small male	adult female	sub-adult	total
lean season 1991					
devil	6	6	12	8	32
spotted-tailed quoll	3	1	2	0	6
eastern quoll	4	4	2	1	11
lean season 1992					
devil	4	2	12	9	27
spotted-tailed quoll	3	1	1	0	5
eastern quoll	2	4	0	0	6
fat season 1990-91					
devil	9	6	20	27	62
spotted-tailed quoll	3	1	2	3	9
eastern quoll	9	10	6	2	27
fat season 1991-92					
devil	8	6	19	37	70
spotted-tailed quoll	5	1	2	1	9
eastern quoll	4	9	4	0	17

Table 3.10 Survivorship of adults and sub-adults of the three species of carnivores at Cradle Mountain at the lean (July - October) and fat (November - January) times of year. As per *Table 3.9*, last few months of data not used. The raw data are presented for individual population classes because sample sizes are too small for calculation of percentages.

	number survived/number present				percent survivorship		
	adult male	small male	adult female	sub-adult	all adults	sub-adults	total
lean season 1991							
devil	4/6	5/6	12/12	9/9	89	100	91
spotted-tailed quoll	3/3	1/1	0/1	1/1	80	100	83
eastern quoll	2/4	3/4	2/2	0/1	70	0	64
lean season 1992							
devil	3/4	2/2	9/12	8/9	78	89	82
spotted-tailed quoll	1/3	1/1	1/1	0/0	60	-	60
eastern quoll	0/2	1/4	0/0	0/0	17	-	17
fat season 1990-'91							
devil	5/9	3/6	11/19	13/27	56	48	53
spotted-tailed quoll	1/3	0/1	1/2	2/3	33	67	44
eastern quoll	1/8	3/11	1/5	1/3	21	33	22
fat season 1991-'92							
devil	4/9	2/6	7/19	12/36	38	33	36
spotted-tailed quoll	2/5	0/1	0/2	1/1	25	100	33
eastern quoll	0/4	1/9	0/4	0/0	6	-	6

3.3.2.2 Evidence of adaptations to food stress

Body condition

There is strong evidence that body condition of male devils changes during the year when pes is used as the linear measurement for comparison with weight (one-way ANOVA, F=3.35, df=5, p=0.02). There is a tendency towards significance and similar trends when the less precise measure, hind leg, which analyses revealed to be a better indicator of overall size of devils than pes (Section 2.2.1.1), is used as the linear measure (one-way ANOVA, F=2.43, df=5, p=0.06). Tukey HSD post hoc tests on the pes data show the differences to be between May/June, when body condition plummets to a low point just for these two months, and November to February when body condition is highest for the year (*Figure 3.2*). As body condition remains high all year except for May/June, I attribute the brief drop in condition to after effects of the mating season which occurs from late February to early April.

No significant changes in body condition during the year are demonstrated for female devils for either measurement, although the pes tends toward the same trend as the males (one-way ANOVA; pes: F=1.76, df=5, p=0.13; hind leg: F=0.66, df=5, p=0.66) (*Figure 3.2*). These analyses indicate that pes is the best measurement to use for calculation of the body condition index in devils.

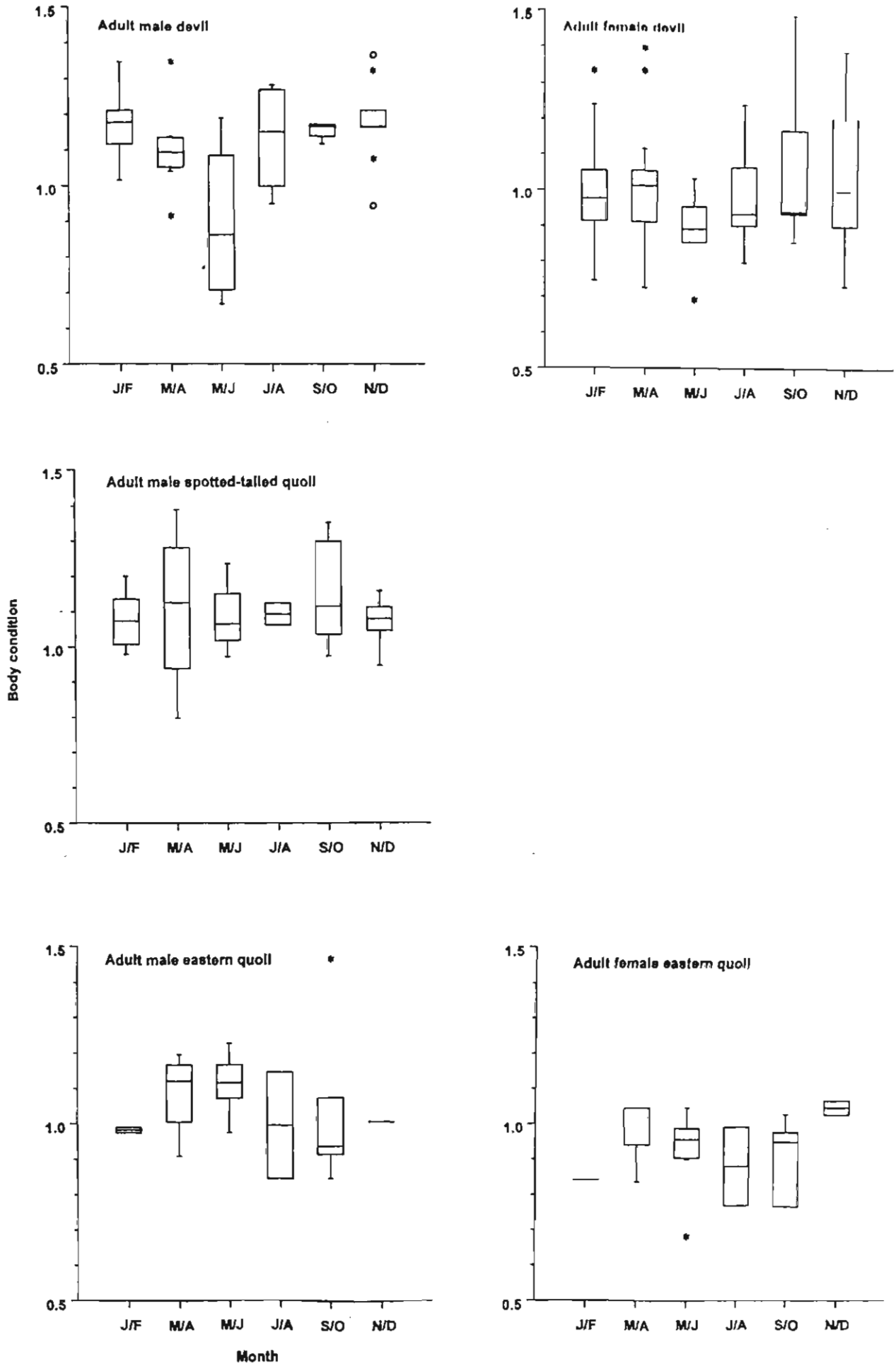


Figure *3.2* Body condition throughout the year for adult devils, spotted-tailed quolls and eastern quolls. Symbols follow Wilkinson et al. (1992).

Body condition of male spotted-tailed quolls does not change significantly during the year (one-way ANOVA, F=0.946, df=5, p=0.47). There is, however, a trend, with highest body condition in late summer (March/April), with a drop during the breeding season in May/June and a steady climb back up over the remainder of the winter (*Figure 3.2*). Similar to what occurs in male devils, body condition appears to be affected more by the mating period than by season. There are not enough data for females for analysis.

In male eastern quolls, there is a clear trend in body condition that appears to be seasonally related. Body condition peaks between late summer and early winter, March to June, drops in July/August and reaches its lowest point in September/October (*Figure 3.2*). This trend is statistically significant when head width, the measurement that best represents overall body size of eastern quolls, is used as a linear measure (one-way ANOVA, F=2.68, df=5, p=0.047) but not when the more precise pes measurement is used (one-way ANOVA, F=1.09, df=5, p=0.39). This pattern is consistent with the seasonal cycle with July to October being the most environmentally stressful time of year. The drop in body condition after the mating season of May/June cannot be separated from the seasonal effects. However, males of the other two species picked up in condition by the next bi-monthly sampling session, even though it is mid-winter. This supports the hypothesis that body condition is seasonally affected in male eastern quolls. This result and the results for male devils suggest that even when the measurement that best predicts body size is known for a species, it is useful to take several different measurements.

Body condition data for female eastern quolls shows no easily explained trends and no significant changes in body condition through the year (*Figure 3.2*) (one-way ANOVA; pes: F=1.42, df=5, p=0.27; head width: F=0.79, df=5, p=0.57). The data for females, therefore, does not support the hypothesis of seasonal effects on condition for male eastern quolls. Late lactation, which occurs in late winter and early spring is likely to affect female body condition more than the mating season. This hypothesis is not supported by the data either.

Food caching

No evidence of food caching by devils was found. The experiment conducted to investigate this was not run in a way that could have involved either of the quoll species. The carcasses were put out in the middle of the night where several devils had been observed feeding for the previous two nights and no quolls had been seen. Carcass remains were all consistent with devil feeding.

Of the six possum carcasses spooled, five were nearly completely eaten, with only the intestines (four cases) or bone chips and fragments of flesh remaining. These carcasses had been carried and dragged through the forest (tall eucalypt overstorey, with a dense shrub layer at 4m and a mixture of clear and dense shrubs at ground level) in a zigzag fashion, with occasional evidence of feeding activity along the route. For three of these, the spool was found. Distances travelled until complete consumption of the carcass and the discovery of the spool were 50 ,30 and 100m. In the two cases where the spool was not found, evidence of the meal was on the ground but the thread was broken at 80 and 170m respectively. It is not unrealistic that the remaining spool may have been swallowed.

The remaining possum was dragged only 15m and left on the ground with one hindquarter partially eaten. There was no attempt to carry off, bury or otherwise conceal it.

Of the observations of the three species of marsupial carnivores feeding on carcasses, no attempt was seen by either species of quoll to remove pieces of carcass (there were very few observations for spotted-tailed quolls), even though eastern quolls would return to a carcass repeatedly throughout the night to feed for long periods. Devils would race off with any pieces they were able to detach and it is not known whether they were eaten or buried. The above experiment is not conclusive but does suggest that caching of food by devils is not a common occurrence.

Body temperature and activity

Both devils and eastern quolls remained homeothermic and maintained the same activity patterns year round, including during the most severe winter weather conditions they would be likely to encounter in their distributional range (deep snow, -8°C, gale-driven sleet and snow, for weeks at a time). No evidence of torpor was found. The availability of food during the study was unknown. The typical pattern for small mammals, for energy conservation, is to go into torpor at intermediate temperatures under food restriction (Hudson, 1978). It is unknown whether eastern quolls would exhibit torpor under these conditions. (Refer to attached draft manuscript Jones; Grigg & Beard, manuscript))

It is also interesting that no differences in length of the nightly activity period were observed for eastern quolls or devils despite a difference in night length from eight hours in mid-summer to fifteen hours in mid-winter (Jones, Grigg & Beard, manuscript).

3.3.2.3 Differences in diet and diet overlap between seasons

Within species

Diet of both large adult male and adult female devils differs significantly between lean and fat times of year (Mantel Test, male $p= 0.002$, female $p= 0.001$). Large mammals constitute a greater percentage of the biomass of the diet for both sexes in the fat season and medium-sized mammals do in the lean season of late winter-early spring (*Table 3.11*). There are no significant differences in the diet between males and females in either the lean season (Mantel Test, $p= 0.22$) or the fat season although there are differences apparent in the fat season which almost reach significance (Mantel Test, $p= 0.03$). Critical minimum p value for this set of four tests is 0.013 (Bonferrroni).

Diet overlap between small and large adult males, and between small adult males and adult females is analysed for the fat season only. Because there are differences apparent in the diet between large adult males and females for the fat season that almost reach significance and the Bonferroni procedure used to set the p value is conservative, any differences in diet between small adult males and other adult devils

are more likely to be detected in the fat season. Diet of small adult males overlaps with that of adult females (Mantel Test, p= 0.20) but is significantly different from that of large adult males (Mantel Test, p= 0.001). A larger proportion of medium-sized mammals, as opposed to large mammals, are found in the diet of small adult male devils than are found in the diet of females. Likewise, medium-sized mammals, instead of large mammals, comprise a greater proportion of the diet of females than large adult males (*Table 3.11*). Therefore, although the differences between large adult males and adult females, and between small adult males and adult females are not significant, the difference between small and large adult males is.

Table 3.11 Diet of male and female devils in lean and fat seasons.

Mean percentage biomass	adult male - lean (%)	adult male - fat (%)	adult female - lean (%)	adult female - fat (%)	small male - fat (%)
large mammal	45	77	25	61	42
medium mammal	55	21	58	37	56
small mammal	<1	<1	7	1	1
tiny mammal	0	0	0	0	0
large bird	<1	2	3	1	1
small bird	0	<1	7	<1	<1
snake	0	0	0	<1	0
skink	0	0	0	0	0
crayfish	0	0	0	0	0
small invertebrate	0	0	0	0	0
No. individuals	11	17	15	34	13

Statistical significance: Mantel Test
(critical p value (Bonferroni) = 0.013)

male devil, lean:fat, p=0.002
female devil, lean:fat, p=0.001
male:female devil, lean, p=0.22
male:female devil, fat, p=0.03
small male:adult male devil, fat, p=0.001
small male:female devil, fat, p=0.20

Diet is not quite significantly different between male and female spotted-tailed quolls in the fat season (Mantel Test, p= 0.01)(Bonferrroni critical p value is 0.013). This may be a Type II error. If sample sizes were larger for females, this result would almost certainly be significant. The diet of females is comprised primarily of small mammals and birds, while that of males is comprised mostly of medium and large-sized mammals (*Table 3.12*). This is consistent with the difference found between the sexes when all data are pooled for the year (section 3.3.1.1). No significant differences are found in the diet of spotted-tailed quolls between lean and fat seasons when sexes are analysed separately (Mantel Test, males p=0.720; females p=0.501) or combined, or between the sexes in the lean season (Mantel Test, p=0.22). There were so few female spotted-tailed quolls trapped and these individuals were caught so infrequently that there are few dietary records with each individual only represented by one or two scats. When the data are divided into seasons, sample sizes are so low and dietary overlap within the group being tested (ie. within females/fat season) is so low that differences cannot be detected using the Mantel Test (see

discussion in Methods section 3.2.3.2 and *Minimum representative sample sizes*, section 3.3.1.1). Reducing prey categories to six makes little difference to the result. The diet of a high proportion of individuals (ie. records) are still represented by only one prey category. Sample sizes (number of different individuals) for these are male/lean, 6; male/fat, 11; female/lean, 3; female/fat, 4. Fortin & Gurevitch (1993) recommends using sample sizes of more than twenty. For the comparison with the most data, male lean/fat (n = 6/11), there are still no discernible differences in the diet between lean and fat seasons.

There are too few data for small adult male spotted-tailed quolls to incorporate into the above analyses. There are only two individuals in the fat season and one in the lean. This would not improve the chance of detecting seasonal differences.

Table 3.12 Diet of male and female spotted-tailed quolls in lean and fat seasons.

Mean percentage biomass	adult male - lean (%)	adult male - fat (%)	adult female - lean (%)	adult female - fat (%)
large mammal	32	39	0	20
medium mammal	47	40	28	0
small mammal	5	9	67	29
tiny mammal	<1	4	2	2
large bird	14	2	0	23
small bird	2	6	2	26
snake	0	0	0	0
skink	<1	0	0	<1
crayfish	0	0	2	0
small invertebrate	0	0	0	0
No. individuals	6	11	3	4

Statistical significance: Mantel Test (critical p value (Bonferroni) = 0.013)	male spotted-tailed quoll, lean:fat, p=0.72
	female spotted-tailed quoll, lean:fat, p=0.50
	male:female spotted-tailed quoll, lean, p=0.22
	male:female spotted-tailed quoll, fat, p=0.01

The story is similar for eastern quolls. No significant differences are found between seasons, when sexes are analysed separately (Mantel Test, males p=0.72; females p=0.31) or combined (including small adult males to boost sample sizes) (Mantel Test, p=0.22), or between sexes within seasons (Mantel Test, fat p=0.54; lean p=0.92). For the two comparisons where there is the most data, 1) between sexes/fat season; in the fat season a higher proportion of medium-sized mammals are found in the diet of males than in that of females and the diet of females is comprised of more small birds and skinks than that of males, and 2) lean/fat seasons; when males are analysed alone and when both sexes are combined the diet of eastern quolls in the fat season is comprised of more invertebrates and fewer small and medium-sized mammals. The reverse is true in the lean season (*Table 3.13*). This is a sensible result as invertebrates are not as available in winter. A significant result might be expected when all adult animals were combined as sample sizes are respectable, but the diet of eastern quolls is so diverse and so variable from scat to scat that a large

number of scats and individuals may be required to detect differences (see discussion in Methods section 3.2.3.2 and *Minimum representative sample sizes*, section 3.3.1.1).

Table 3.13 Diet of male and female eastern quolls in lean and fat seasons.

Mean percentage biomass	adult male - lean (%)	adult male - fat (%)	adult female - lean (%)	adult female - fat (%)	all adults - lean (%)	all adults - fat (%)
large mammal	0	0	0	0	0	0
medium mammal	14	19	22	11	26	14
small mammal	26	12	47	24	31	16
tiny mammal	1	11	0	1	<1	5
large bird	0	7	12	10	2	5
small bird	17	11	15	18	11	13
snake	7	<1	0	2	3	3
skink	34	19	4	16	27	22
crayfish	0	5	0	<1	0	4
small invertebrate	<1	16	0	18	<1	18
No. individuals	6	19	3	6	16	45

Statistical significance: Mantel Test (critical p value (Bonferroni) = 0.013)

male eastern quoll, lean:fat, p=0.72
female eastern quoll, lean:fat, p=0.31
male:female eastern quoll, lean, p=0.92
male:female eastern quoll, fat, p=0.54
all adult eastern quolls, lean:fat, p=0.22

Changes in niche breadth with season

An analysis of change in niche breadth with season was carried out only for devils, because no significant differences in diet were found for either quoll species. The normalised (*B*) index for ten prey categories was as follows: males in lean season *B*=0.201, males in fat season *B*=0.158, females in lean season *B*=0.244, females in fat season *B*=0.194. This implies that niche breadth is greater in the lean season. Close examination of the data reveals that the diet is more equitable in terms of available resources in the lean season. The switch to larger mammals in the fat season represents a specialisation of diet, because more of the diet is concentrated in one category (*Table 3.11*).

Between species

Because there are seasonal differences in the diet of both sexes of devils and are probably seasonal differences in the diet at least of male spotted-tailed quolls (statistical significance was probably obscured by small sample sizes) there is justification for comparing diet overlap between devils and spotted-tailed quolls on a seasonal basis. Diet between the sexes for both species is not significantly different for either the fat or lean season, but there is a trend of difference in the fat season. Therefore, the sexes are separated and analysis is restricted to a comparison of the

diet of male spotted-tailed quolls and female devils in the fat season. The lack of significant differences between the sexes means that theoretically the sexes should be combined, but because a trend is apparent in the data, combining sexes in the analysis may have obscured any real differences.

Diet of female devils and male spotted-tailed quolls overlapped significantly (ie. no significant difference Mantel test, p=0.25) in the lean season but were different in the fat season (Mantel test, p=0.001). This is probably mostly a result of female devils switching to a larger proportion of large mammals in their diet in the fat season (*Table 3.14*).

Table 3.14 Diet of adult female devils and large male spotted-tailed quolls in the lean and fat seasons.

Mean percentage biomass	female devil - lean (%)	male spotted-tailed quoll-lean (%)	female devil - fat (%)	male spotted-tailed quoll-fat (%)
large mammal	25	32	62	39
medium mammal	58	48	37	41
small mammal	7	5	<1	9
tiny mammal	0	<1	0	4
large bird	3	14	<1	2
small bird	7	2	<1	6
snake	0	0	<1	0
skink	0	<1	0	0
crayfish	0	0	0	0
small invertebrate	0	0	0	0
No. individuals	15	6	34	11

Statistical significance: Mantel Test (critical p value (Bonferroni) = 0.025)
female devil: male spotted-tailed quoll, lean, p=0.25
female devil: male spotted-tailed quoll, fat, p=0.001

The comparison between spotted-tailed quolls and eastern quolls for the lean season and the fat season is not calculated. Because there is a significant difference in the diet of male and female spotted-tailed quolls both over the fat season and over the whole year, the comparison would need to be done between female spotted-tailed quolls and eastern quolls (for which no sex differences in diet were found). Prior analyses demonstrated that sample sizes for female spotted-tailed quolls are too small for differences to be detected.

3.3.3 Den use overlap

There is no indication that any of the three species use the same size or type of den. The small sample size for spotted-tailed quolls precluded statistical validation, but there were large differences in tunnel dimensions, habitat type and siting of dens with respect to topography for each species (*Tables 3.15* and *3.16*).

Devil dens are much larger than dens of either of the two quoll species. They were mostly sited well within wet eucalypt forest on moderate slopes, all were in forest of some kind.

The one spotted-tailed quoll den for which the entrance was found had a larger tunnel than the average tunnel dimensions for eastern quolls. Dens of the two quoll species were in very different habitat situations. Both spotted-tailed quoll dens found were situated on steep slopes near cliffs in dense, dry scrubby eucalypt forest. These were located by radiotracking collared animals; the entrance to the second den was never found. One was at the base of a twenty metre high cliff, the other was situated between a three metre high cliff and the top of an eight metre waterfall in a canyon. By contrast, eastern quoll dens were typically in flat country in grassland or in rainforest that bordered on grassland (within one hundred metres of the edge).

Quoll dens (both species) and most devil dens were underground burrows dug in soil, often under a log or into the base of a rotten or hollow stump. Some devil dens were caves in the base of low cliffs (one to three metres high) and earthen dens were often flanked by boulders or tree roots. Both devils and eastern quolls denned under buildings at Cradle Mountain, devils under the dining room of the Cradle Mountain Lodge (a large tourist accommodation) and eastern quolls in the middle of a large woodshed (always kept at least half full). Spotted-tailed quolls are also known to den under buildings.

Table 3.15 Dimensions of den entrances of the carnivores at Cradle Mountain.

	N	Height (cm): mean (range, sd)	Width (cm): mean (range, sd)	No. entrances: mean (range, sd)
devil	19	28.6 (17-38, 5.4)	33.1 (13-53, 9.7)	1.4 (1-3, 0.6)
spotted-tailed quoll	1	16	20	1
eastern quoll	9	13.2 (8-20, 4.4)	17.9 (9-26, 5.5)	1.7 (1-3, 0.8)

Table 3.16 Habitat situation of dens of the carnivores at Cradle Mountain.

	N	percent in rainforest	percent in wet eucalypt forest	percent in dry eucalypt forest	percent in grassland	Slope: mean (range, sd)	Distance to forest verge: mean (range, sd)
devil	21	24	52	24	0	13.8 (0-40, 11.2)	99.5 (5-700, 154.2)
spotted-tailed quoll	2	0	0	100	0	25 (10-40, 21.2)	15 (0-30, 21.2)
eastern quoll	7	43	0	0	57	5.7 (5-10, 1.9)	in forest: 76.6 (50-100, 25.2) in grassland: 45.0 (30-120, 63.6)

3.4 Discussion

3.4.1 Patterns of diet overlap, prey size, fractal dimensions of the habitat and sexual dimorphism

While diet between each of the three species did not overlap when the sexes of each were combined, the only difference found between adjacent morphospecies was between male and female spotted-tailed quolls. It appears that the carnivore guild divides into two groups based on diet; devils and male spotted-tailed quolls which consume mostly larger prey species, the medium and large-sized mammal categories comprised of possums, wallabies and wombats, and female spotted-tailed quolls and eastern quolls which consume mostly smaller prey species, small mammals up to the size of sugar gliders, birds, reptiles and invertebrates. This division follows the discontinuous natural size distribution of the assemblage of the mammalian species at Cradle Mountain.

Holling (1992) found that size-clumps or discontinuities in body mass distributions are universal in animal assemblages in terrestrial ecosystems. These clumps occur because animals have attributes of size and behaviour that are shaped by the discontinuous but hierarchical architecture of the landscape in which they live. Thus the geometry or fractal dimensions of the landscape and ecosystems and hence habitats shape the morphology of animals. There are ranges of body size at which animals can use a particular spatial scale or fractal dimension of the habitat. The gaps in body size distribution relate to the zone or no man's land between two spatial scales. There are no animals of the body size range represented by these gaps because they would be too large to operate at the dimensions of the next spatial down and too small to survive and function at the dimensions of the next largest spatial scale. The more structurally complex the environment is, the more size clumps that exist. The mammal fauna at Cradle Mountain falls into two significant size-clumps, smaller mammals which include all mouse and rat-sized mammals up to the size of and including the sugar glider, and larger mammals which include the range from ringtail possums up to wombats. There is a significant size gap between sugar gliders and ringtail possums. (see also section 3.2.3.2, paragraph 7)

A very interesting finding of this study is that not only do the patterns of dietary overlap among the morphospecies of the guild of carnivores relate directly to the size-clumping of their prey species, which relates to the fractal dimensions of the habitat, but that the split between the two dietary groups of carnivores, those that eat large prey and those that eat small prey, occurs between the sexes within a species. A general division of vertebrate carnivores into those that eat large prey and those that eat small prey is well documented (Peters, 1983; Vezina, 1985), and the size differences in prey of male and female mustelids, which exhibit extreme sexual size dimorphism, are well known (Day, 1968). This is the first time that large differences

in prey size between sexes of a species have been related to the size distribution of the prey species.

It is interesting that sexual dimorphism in body mass is much more pronounced in spotted-tailed quolls (94%) than in either devils (56%) or eastern quolls (56%). It seems as though these patterns in dimorphism relate to the patterns in diet overlap and size-clumping of prey species. However, selection resulting from competition for food resources should operate on the trophic characters proximal to the foraging and feeding behaviour of the species, in this case canine strength, not on body size (Dayan *et al.*, 1989a; 1992). Many factors select for body size (Peters, 1983). In fact, competitive character displacement does influence the size of canine strength in the quolls in Tasmania. An evolutionary shift has occurred in canine strength for both sexes of both species of quolls in Tasmania resulting in morphological patterning in the form of equal size ratios (Chapter 2). This has also resulted in a reduction in sexual size dimorphism in canine strength in both quoll species in Tasmania. This reduction is more pronounced in spotted-tailed quolls (a reduction of 14% from 67% on the mainland to 53% in Tasmania) than in eastern quolls (a reduction of 8% from 59% to 51%). The degree of size dimorphism in canine strength for devils is smaller at only 31% (*Table 2.4*). So, without the operation of character displacement, spotted-tailed quolls exhibit the greatest degree of sexual size dimorphism in canine strength as well as in body mass. Weak patterning was found in prey size that supported the hypothesis that competition for food was the causal factor underlying the patterning in canine strength. It was the much larger prey of the adult male spotted-tailed quoll relative to the regular increases in prey size among the three smaller morphospecies, the female and male eastern quoll and the female spotted-tailed quoll, that weakened the patterning.

A summary of these complex processes is as follows: The hierarchical geometry or fractal dimensions of the habitat shapes the body size of the prey species causing two size-clumps to evolve. The three species of carnivores evolved at three different sizes whose prey size utilisation covered the entire range of prey sizes. The prey size range of the spotted-tailed quoll bridged the gap between the two size-clumps of prey. As a result of this, sexual size dimorphism in body size, including body mass and canine strength, is greater in spotted-tailed quolls than in either devils or eastern quolls. This occurs both in Tasmania and on the mainland where the devil is extinct. In Tasmania, however, the presence until very recently of two larger species of carnivores may have added an extra pressure on prey resources, resulting in competitive character displacement in the two most similar species, the congeneric quolls. Character displacement has operated on canine strength, resulting in equal size ratios between adjacent morphospecies. The effect of this has been to reduce the degree of sexual size dimorphism in canine strength in both species of quolls in Tasmania compared to the mainland, although the reduction has been greater in spotted-tailed quolls. This presumably has reduced competition between the two species. If competition is the underlying causal factor, the size of canine strength should determine the size of prey that the morphospecies eats. There is some evidence to support this. Prey size increases with body size and there is weak patterning in prey size. However, evidence from patterning in prey size can only be weak because the prey size range utilised by the three smaller morphospecies are in the small size-clump and the prey size range used by the largest of the four

morphospecies, the male spotted-tailed quoll is in the large size-clump. Thus there is a gap in prey size so strong patterning or equal size ratios in prey size cannot occur.

3.4.2 Seasonal changes in diet overlap

Having found overlap between both sexes of spotted-tailed quolls and the adjacent species, a search was made for indications that food may be limiting at the most environmentally stressful time of year. This is the period when competition is more likely to occur or to be more intense. For the duration of the field study at Cradle Mountain this period was thought to be late winter/early spring, July to October. This is at the end of the winter period of low plant growth and the weather is at the harshest, with cold fronts every few days bringing sleet, snow and constant wind-driven rain. Snow could lie on the ground for up to three weeks. This was the main time of year when herbivores such as macropods were observed to be in poor condition and were found dead. Although a proper assessment of food limitation was not within the scope of the project, periods during the year when animals appeared to be more hungry than at others, the existence of behavioural and physiological mechanisms to cope with food shortage or increased energy demands and physiological mechanisms to conserve energy would indicate that food may be limiting.

Analysis of carcass consumption at different times of year did not indicate that animals were more hungry in winter. No evidence was found of higher mortality in winter. Body condition, a mechanism whereby fat stored in summer could be utilised in winter, did not show any seasonal trends other than those associated with the mating period for males. Both eastern quolls and devils remained homeothermic year round and they maintained the same length of activity period each night regardless of the large differences in day length between summer and winter. Torpor as an energy conserving mechanism did not appear to be a normal part of their winter biology. Finally, investigations showed that at least devils do not regularly cache food in winter, as a means of storing food for later use. In conclusion, no indirect evidence that the carnivores at Cradle Mountain were particularly hungry or stressed by food scarcity at any time of year was found.

Although no evidence of a food-limited or environmentally stressful time of year was found, the diet of devils and probably also that of eastern quolls (small sample sizes may have affected the power of the test to detect differences) changes between late winter/early spring (the lean or most environmentally stressful time of year) and the remainder of the year (fat season). Both sexes of devils switched to a higher percentage by biomass of large mammals in their diet in summer compared to a biomass composed more of medium-sized mammals in the lean time. This shift is more accentuated in males than females although the difference between sexes in the fat season is not quite significant. The switch to large mammal species in the fat season may represent a switch not to consuming larger prey items but to capitalising on the influx of juvenile wombats and Bennett's wallabies in summer.

The result of this shift is that adult male spotted-tailed quolls overlap with devils in the lean season (July to October) but not in the fat season (November to June). However, in the fat season, the large annual cohort of young devils overlap in body weight and in diet with male spotted-tailed quolls. This period also coincides with

the time of year in this strongly seasonal environment when young of all species - predator as well as prey - emerge. Some of the pressure of the large influx of young devils may be absorbed by the influx of inexperienced juveniles of the prey species. There is however, no time of year when male spotted-tailed quolls do not overlap in diet with devils. Conversely, adult devils are free from overlap with an adjacent species for more than half of the year.

Unfortunately, there are insufficient data to repeat this analysis for female spotted-tailed quolls and eastern quolls where body weight between sub-adult spotted-tailed quolls overlaps that of male eastern quolls for a similar period of the year. However, extrapolating from the available data, I suggest that female spotted-tailed quolls, which are major predators of small mammals, birds and some larger mammals, would overlap more in diet with eastern quolls in the lean season, when eastern quolls consume more small and medium-sized mammals, than in the fat season or summer, when eastern quolls switch to a higher proportion of invertebrate prey. It can be speculated that juvenile and sub-adult spotted-tailed quolls, which are of a similar size to eastern quolls, would overlap in diet with at least male eastern quolls in the fat season, from November to June. It can be further speculated that if more data were available, the story of the male spotted-tailed quoll/devil overlap would be repeated, with a difference that the degree of overlap with adjacent species would be less for the female than for the male spotted-tailed quolls. The female spotted-tailed quolls would overlap in diet with eastern quolls for at least part of the year, probably less in summer, and young spotted-tailed quolls would overlap with eastern quolls. Although they overlap in body weight with female spotted-tailed quolls, juvenile devils are definitely carnivores of larger mammals and so overlapped with members of this group, namely male spotted-tailed quolls and female devils. Morphologically, of course, even the small juvenile devils are of a more robust build with stronger jaws than female spotted-tailed quolls. Eastern quolls would overlap with young and/or adult female spotted-tailed quolls for the entire year but young eastern quolls would be free of direct overlap with a guild member.

The seasonal changes found in diet for devils (switch to larger prey species in the fat season that possibly represents a switch to the juveniles of the larger prey species rather than a switch to larger prey) and eastern quolls (consumption of more insects in summer) represent a switch to prey items not available in winter. It does not really reflect a change between specialisation and opportunism. In fact, devil diet is more specialised in the fat than in the lean season. According to Wiens (1993), we might expect niche overlap to decrease as animals specialised in their diet in the relatively lean period of winter, provided resources were becoming limited. As no indications were found that any of the carnivore species at Cradle Mountain were food or environmentally stressed at any time of year, this may merely reflect the observation from Jaksic's study (cited in Wiens, 1993), of hawk, owl and fox predators in a semi-arid scrub desert in Chile, that for guilds of predators that rely on mammalian prey, as opposed to insect prey, 'lean' and 'fat' periods were expressed on a scale of years not seasons (Wiens, 1993). The two and a half years of this field study were not sufficient to detect these kinds of differences. This study provides some support for Wiens's contention that the 'fat-lean' scenario may be an oversimplification.

3.4.3 Den use

It is very obvious that each of the three species uses quite different sized dens, that relate closely to their body size, and different den situations, so the chance for competition for den sites would be negligible. It is questionable whether sites for burrows in the ground could ever be limiting, although sites that are suitably drained in the very wet environment at Cradle Mountain may be limited and social behaviour within and between species may limit the permissible minimum distance between dens. Of interest though, was the overlap in den use between devils and wombats, with tracks of both species going into and out of the same den entrance in the same night. Some devil dens, by their situation in cliffs and dense scrub, in the size and structure of the entrance hole and in the complete lack of evidence of wombat activity, such as scats, appeared to be exclusively constructed and occupied by devils. Other devil dens had a similar appearance to active wombat burrows, with the tunnel entrance deep down in a large mullock heap. With reference to badger sets that were recorded in the Domesday Book in 1086 and are still active today, I suggest that the large burrows that are used by devils and wombats may be very old, perhaps centuries old. Successive generations of occupants may alter and extend them and they may pass successively between the two species. As devils attack and eat wombats (see Chapter 2), and wombats are known at least by popular lore to be able to crush dogs to death in the tunnels, it is unlikely that both species would cohabit unless the burrow systems are extensive enough to enable each species to occupy different parts. No other resources that could be limiting to the three species of carnivores were identified.

3.5 Summary and conclusions

To summarise, the spotted-tailed quoll species, with sex and age classes combined, would experience the highest degree of dietary or resource use overlap of the three species. Devils would experience the least degree of overlap. Because no data or model exists of the resource requirements of the carnivores or of resource availability, at best inferences only can be drawn that the degree of overlap suggests that spotted-tailed quolls are likely to suffer more from competitive effects than do the other two species. This may explain the disparities in relative abundance between the three species with the spotted-tailed quolls being rare. Although no indications of a food limiting time of year were found, food limitation may not occur on the time scale on which this project was run. Intraspecific competition or density effects, which may be stronger than relationships between species (MacNally, 1983), have not been taken into account. Indications are that these could be strong for devils, with interference over the large food items which comprise the bulk of their diet (see Chapter 5). This is reinforced by evidence that the diet of young devils, both sub-adult and juvenile, resembles that of adult devils more closely than it does spotted-tailed quolls. This result is consistent with studies on other taxa which indicate that although body size may overlap, differences between age classes of a species are usually less than those between species (Polis, 1984). The degree of overlap within species suggests that intraspecific competition may be less important for spotted-tailed quolls than for the other two species. Also not considered are the effects of intraguild predation and cannibalism. Fur of all three carnivore species was found in

devil scats and eastern quoll fur was found in eastern quoll scats. Whether these were predated or cannibalised is not known. Devils have been observed to start dining on a less fortunate individual that has just been run over by a car, even before the carcass has cooled.

Taking the question further of whether interspecific competition for food influences species abundance requires perturbation experiments where numbers of the three species are manipulated. Even changed patterns of resource use in allopatry and sympatry with different species is not evidence of either coexistence by resource partitioning or of competition (MacNally, 1983). Such experiments at the scale of these medium-sized mammalian carnivores would be extensive and expensive.

Chapter 4 Habitat partitioning of sympatric devils, spotted-tailed quolls and eastern quolls

4.1 Introduction

Differential use of resources among guilds of ecologically similar species is well documented for a wide range of taxa (Schoener, 1968; 1986; Pianka, 1975; Smith *et al.*, 1978; Emmons, 1980; Abrams, 1987; Gordon & Illius, 1989), including mammalian carnivores (Rosenzweig, 1966; Rautenbach & Nel, 1978; Simms, 1979; Bothma, Nel & MacDonald, 1984). Competition is thought to be the major factor causing niche differentiation and the consequent morphological and behavioural differences between the species (Hutchinson, 1959; MacArthur & Levins, 1967; Pianka, 1974; 1975; Diamond, 1975; Schoener, 1986). Niche differentiation will therefore reduce competition between species. Habitat is the niche parameter most commonly partitioned in animals, with food coming second (Schoener, 1986). Time is rarely partitioned and may not be effective in reducing exploitation competition (Jaksic, 1982; Schoener, 1986). A survey of resource partitioning in animals showed that in nearly all guilds studied several niche dimensions, usually two or three, are important in separating species (Schoener, 1974). Schoener (1974; 1986) proposed two generalisations based on patterns in species differences. Firstly, the number of niche dimensions on which partitioning is occurring should increase with the number of species in the guild, and secondly, species that are similar on one dimension such as food should differ on another, for example, habitat use.

It has been demonstrated in this study that competition for food is likely to be an important structuring force in the marsupial carnivore guild in Tasmania (Chapter 2). There is evidence of partitioning of the food resource, based on prey size, although there is substantial overlap in diet between eastern quolls and female spotted-tailed quolls, and male spotted-tailed quolls and devils (Chapter 3). The questions should now be asked: 1) do the three species that comprise the marsupial carnivore guild at Cradle Mountain partition habitat as well as food, 2) is there evidence that habitat is partitioned where diet overlaps between morphospecies and 3) what is the relationship between morphological adaptations, prey type and habitat use in these species? Answering these questions are the specific aims of this chapter. Particular attention will be paid to the two groups of species/sex classes (mentioned above) where there is significant overlap in diet, and to the age/sex classes where there is overlap in body weight between species (see section 3.1 for description). Time was not considered a potential niche parameter for partitioning because all predators and most of their prey species are mostly nocturnally active.

Habitat use is often assessed by direct observation of the animals in the field (Schoener, 1968; Emmons, 1980; Gordon & Illius, 1989; McCullough, Hirth & Newhouse, 1989). However, for species which are not easy to observe directly, methods to determine the location of the animal from which its surrounding habitat can be derived are employed. These include the location of the trap in which the animal was caught (Simms, 1979; Dickman, 1986b) and radio-tracking (Amlaner & MacDonald, 1980). There are limitations with interpreting the data derived from both these methods. Attracting animals into traps using food bait may draw individuals

from outside their preferred habitat, thus biasing the results. Radio-tracking gives imprecise information on habitat use unless the observer is at close range, which may influence the behaviour and therefore habitat use of the animal. There is an error polygon in the accuracy of location, which increases with the observer's distance from the radio-tagged individual giving imprecise information on habitat use, that makes a precise estimate of habitat type difficult, especially where blocks of similar habitat are small (Amlaner & MacDonald, 1980). Also, from a distance, it is impossible to determine fine scale habitat use such as arboreal activity. The latter has been overcome by the use of hair sampling tubes to detect arboreal use of habitat (Suckling, 1978; Dickman, 1986a; Dickman, 1986b).

Recently, techniques using spool-and-line tracking devices (Miles, de Souza & Povoa, 1981; Berry *et al.*, 1987; Anderson *et al.*, 1988; Hawkins, 1989; Woolley, 1989) or fluorescent pigments (Lemen & Freeman, 1985) have been developed that give very precise information on an animal's movements. Both these techniques leave a trail where the animal has been, enabling information on fine scale habitat use to be collected. While both have been used for small mammals, only spool-and-line tracking is really suited to larger animals which move large distances. Spool-and-line tracking is not a new technique, having been used sporadically at least since 1927 (Breder, 1927; Stickel, 1950), but it has only gained popularity in the last fifteen years. It can provide very precise and detailed information on movements, habitat use and foraging activity and the devices are cheap and easy to assemble and use. Its limitations are the lack of information on time scales at which the trail is laid, the short amount of time each device lasts and the necessity for catching an individual prior to attachment of the spooling device.

In this study, spool-and-line tracking is used to determine habitat use. Devils and quolls are nocturnal, wary of people and the two larger species live in dense, sometimes rugged forest habitat. They also range many kilometres in a night and can move fast over long distances. In a rugged study area without good access to vantage points and with small, fragmented habitat blocks, radio-tracking would not have yielded detailed or precise enough information on habitat use and direct observation was out of the question. Spool-and-line tracking provides very detailed information on both horizontal and vertical use of the habitat. Different movement patterns can be recognised. In this study, a straight-line pattern of the spool is interpreted as a commuting movement while a weaving or double back pattern is interpreted as foraging (searching for prey or carrion) or chasing prey, respectively. The major limitation was in the short distances, relative to the distance travelled each night, that it was possible to record. The limitation was not on the weight of the device but on its bulk. This will be discussed further in the "Methods" section (4.2).

4.2 Methods

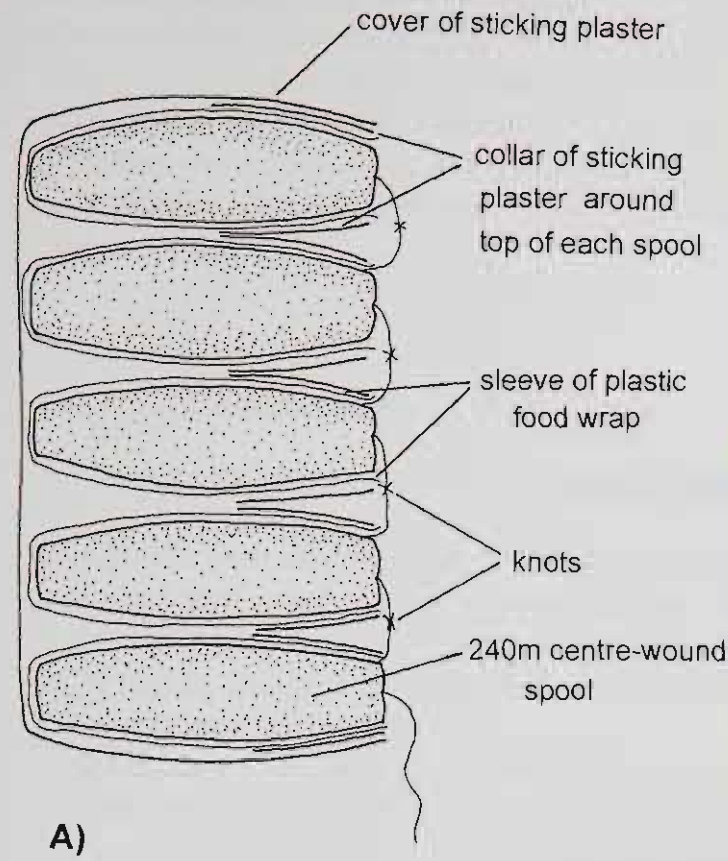
4.2.1 Spool-and-line tracking devices

Spool-and-line tracking devices were constructed following the methods of Andrew Dennis (pers. comm., 1991), modified to suit these study animals and environmental conditions. Centre-wound spools of fine white thread, 240 metres in length (Penguin Threads Australia Pty. Ltd.) are individually wrapped in plastic food wrap (eg. "Glad Wrap"), strapped together in a single row with pharmaceutical sticking plaster (eg. "Elastoplast") and the ends tied together to form a continuous thread (*Figure 4.1*). The plastic wrap serves to prevent the thread from adhering to the sticking plaster and allow free flow. To prevent spools from falling out of the package, each one is strapped to the adjacent spool in addition to a wrap of plaster around the combined spools. Four half knots are tied and the knot dabbed with a quick-setting glue (eg. "Supa-glue") to prevent the knots from slipping apart.

The spool-and-line tracking devices are attached to the fur on the flat, sacral region of the rump of the devil or quoll using quick-setting glue (2 minute "Supa-glue Gel") so that the thread feeds freely out behind the animal, clear of its legs, as it moves (*Figure 4.1*). The guard hairs are trimmed as the glue does not adhere well to them. Long fur is trimmed to half a centimetre in length to prevent the device from moving and distracting the animal as it runs. About ten small dabs of glue are sufficient to hold the device, taking care that they do not soak through and adhere to the skin. It is important to use viscous "Gel" glue.

Animals were trapped as part of the trapping regime described in Chapter 3. Individuals suitable for spool-and-line tracking were left in the trap all day, in the shade covered with a sack. Individuals were not sampled more than once for reasons of statistical independence. The spool-and-line tracking device was attached at dusk and the animal released, after tying the end of the thread to a bush, at point of capture. Only individuals which had been trapped several times and thus were accustomed to being handled were used. All of the thread, starting at the release point, was used for data collection because it was not always possible to determine when the animal stopped fleeing from the trap and started on its night's activities. Most animals seemed to recover in about thirty metres. After an initial straight line dash, the animal usually stopped (could hear this after release) and substantially changed direction (as detected from the thread) within this distance.

The number of spools and hence length of thread attached to each animal depended on its body size. Animals over three kilograms in weight were fitted with five spools totalling twelve hundred metres. This was a package four by seven centimetres and one and a half centimetres thick. Four spools were attached to individuals between two to three kg in weight, three spools if they were between one and a half and two kg and two spools if they were less than one and a half kg in weight. The main factor limiting the length of thread that can be placed on an animal is the bulk of the device; none of the devices even approached the five percent of body weight limit that is the conventionally used as a guide for the maximum weight of radio collars (Amlaner & MacDonald, 1980). A greater length of thread could have been attached, but if too large the device may distract the animal and thus influence its behaviour. Observations of animals carrying spool-and-line tracking



C)

Figure 4.1 Spool and line tracking devices. A) Plan of device for animal over three kilograms in weight, comprised of five spools totaling 1200 m. B) Spool attached to rump of devil prior to release (Photo: Edwin Chester) C) Spotted-tailed quoll leaving a trail of thread just after release (Photo: Dave Watts).

devices indicated they were not aware of the device. None were ever removed or chewed before they ran out. The empty package was generally chewed off by the next night. Another reason for limiting the size of the packages was the time taken to record the data, between four and nine hours for twelve hundred metres of spool. On the short winter days, only one could be recorded. The nature of the terrain made it impossible to leave a spool half recorded and find it again to complete it the following day.

4.2.2 Data collection and analysis

Population classes are used as defined in Section 3.2.2.

Spools were recorded within a couple of days of release except when it snowed and the thread was buried, sometimes for up to a week. The thread was broken by other animals walking through it at night and became difficult to follow after about three nights. Distance is estimated by pacing along the thread. Every ten metres, the following data are recorded:

- vegetation or habitat type - as defined in Section 1.2.
- pattern of the thread in the previous ten metres - straight line movement (commuting) or weaving or doubling back (foraging) pattern
- visibility within half a metre of the ground - A one metre square sighting board was used for calibration. Ranked as 0 (= clear understorey, less than seventy percent of the board was obscured by vegetation or rocks when the observer was looking at the board from half a metre above the ground and ten metres distance), 1 (= more than seventy percent of the board was obscured at ten metres), 2 (= dense understorey, more than seventy percent of the board was obscured at five metres), 3 (= very dense understorey, more than seventy percent of the board was obscured at one metre).
- steepness of slope - ranked as 1 = gentle, 2 = moderate, 3 = steep, 4 = cliff
- number of trees climbed in the previous ten metres and height climbed to
- number of logs encountered in the previous ten metres
- number of logs climbed in the previous ten metres and distance travelled along log
- distance from the nearest forest/grassland ecotone.

These data were collected to examine the type of habitat each morphospecies occupies and forages in and the fine scale components of the habitat that were used (forest verges, vertical component).

Data are summarised as percent of total data recording points in each habitat type, percent of records where the thread is in a foraging pattern in each habitat type, mean of rank scores for visibility and slope, number of trees climbed and number of logs encountered per kilometre of thread, percent of logs encountered that were climbed and percent of distance that was spent arboreal (as in *Table 4.1*) and percent of total distance of spool when the animal was within fifteen metres of a forest edge (as in *Table 4.3*).

All the data, except that for distance from the forest verge, was analysed using a multivariate analysis of variance and canonical variate or discriminant function

analysis. Because most of the dependent variables used in the analysis were correlated, a Principal Components Analysis with Varimax rotation was conducted and the component scores were used as the set of dependent variables. PCAs require the data to be normally distributed and linearly related so, after checking scatter plots, the data were transformed using square root transformations (for count data), arc sine square root transformations (for proportional data) and log transformations (for abundance data). Scores from the MANOVA were submitted to canonical variate analysis. (Tabachnik & Fidell, 1989)

To determine if there is a correlation between the extent of arboreal activity and the percentage of arboreal species in the diet, the percentage biomass diet composition data for the arboreal species was extracted from the medium and small mammal categories (from Chapter 3). The total percent biomass of arboreal prey species (both mammals and birds) was correlated with the percent distance spent above the ground.

4.2.3 Test of tree-climbing ability

To test how well devils can climb, hair sampling tubes (Suckling, 1978 and Debbie Andrews, pers. comm., 1992), modified for devils, were constructed. Made from polypipe and downpipe, they have a single flanged end, eleven centimetres in diameter and fifteen centimetres deep. The bait, comprised of either raw or cooked liver and bacon, is placed behind metal mesh via a screw cap in the back. "Scotch" double-sided sticky tape is placed in four wide strips inside the flange to determine if devils have reached the tube. When devils put their snout into the tube to reach the bait, hairs are left behind on the sticky tape.

The hair sampling tubes were wired onto tree trunks in an area where there was high devil activity. Climbing situations varied from vertical to fifty degree sloping trunks, ranging in diameter from fifteen to sixty centimetres, both with and without small side branches. They were checked at daily and fortnightly (between trip) intervals.

4.3 Results

4.3.1 Habitat analysis

Devils, spotted-tailed quolls and eastern quolls differ significantly in the type of habitat that they both travel and forage in (MANOVA, Pillai Trace=1.379, f=8.138, df=12,44, p<0.001). Patterns for percent distance and percent foraging distance in different habitat types is similar and will not be distinguished in the description of the results. The strongest difference is between eastern quolls and the other two species. Eastern quolls spend much of their time (for ease of expression "time", meaning percent of data points, will be used) and most of their foraging time in grassland, with gentle slopes, high visibility and few obstructions such as fallen logs,

compared to forest for the two larger species. Eastern quolls are much less arboreal than the other two species. The second canonical variate axis separates devils from spotted-tailed quolls. Spotted-tailed quolls spend much more time in rainforest with steeper slopes, denser understorey and more fallen timber than devils, which range and forage in both rainforest and wet eucalypt forest, with a bias towards wet eucalypt forest. Spotted-tailed quolls are also more arboreal than devils, spending ten times the amount of distance above the ground. (*Table 4.1* and *Figure 4.2*)

Several of the habitat components are correlated. High values for visibility and slope correspond with increasingly dense understorey with less visibility and steeper slopes. (*Table 4.1*)

Table 4.1 Percent of total length of spool, and percent of records where the spool was in a foraging pattern, in each habitat type, visibility at half a metre above the ground, steepness of slope, number of logs encountered in habitat and degree of arboreal activity for devils, spotted-tailed quolls and eastern quolls (mean values for the raw data).

	devil	spotted-tailed quoll	eastern quoll
% distance in:			
rainforest	29	56	10
wet eucalypt forest	39	10	0
dry eucalypt forest	14	9	13
mixed forest	11	14	7
grassland	8	11	67
buttongrass	0.1	0	2
% foraging records in:			
rainforest	29	43	9
wet eucalypt forest	34	12	0
dry eucalypt forest	14	33	6
mixed forest	13	7	2
grassland	10	4	79
buttongrass	0.1	1	4
visibility at 0.5m height	0.58	1.06	0.44
slope	1.31	1.59	1.03
no. trees climbed/km	0.17	0.91	0
no. logs encountered/km	10.34	16.85	4.32
% logs climbed	35	71	57
% distance arboreal	1	11	0.1
N	15	7	7

There are no significant differences in habitat use among age/sex classes where body weight overlaps between devils and spotted-tailed quolls (MANOVA, Pillai Trace=0.899, F=1.569, df=18,66, p=0.095). However, because the sample sizes are very small (*Table 4.2*), and MANOVA lacks power at small sample sizes (Tabachnik & Fidell, 1989), the Type II error rate may be high. The trends that are visible in the data (*Figure 4.3*) may be real differences that would be statistically significant if

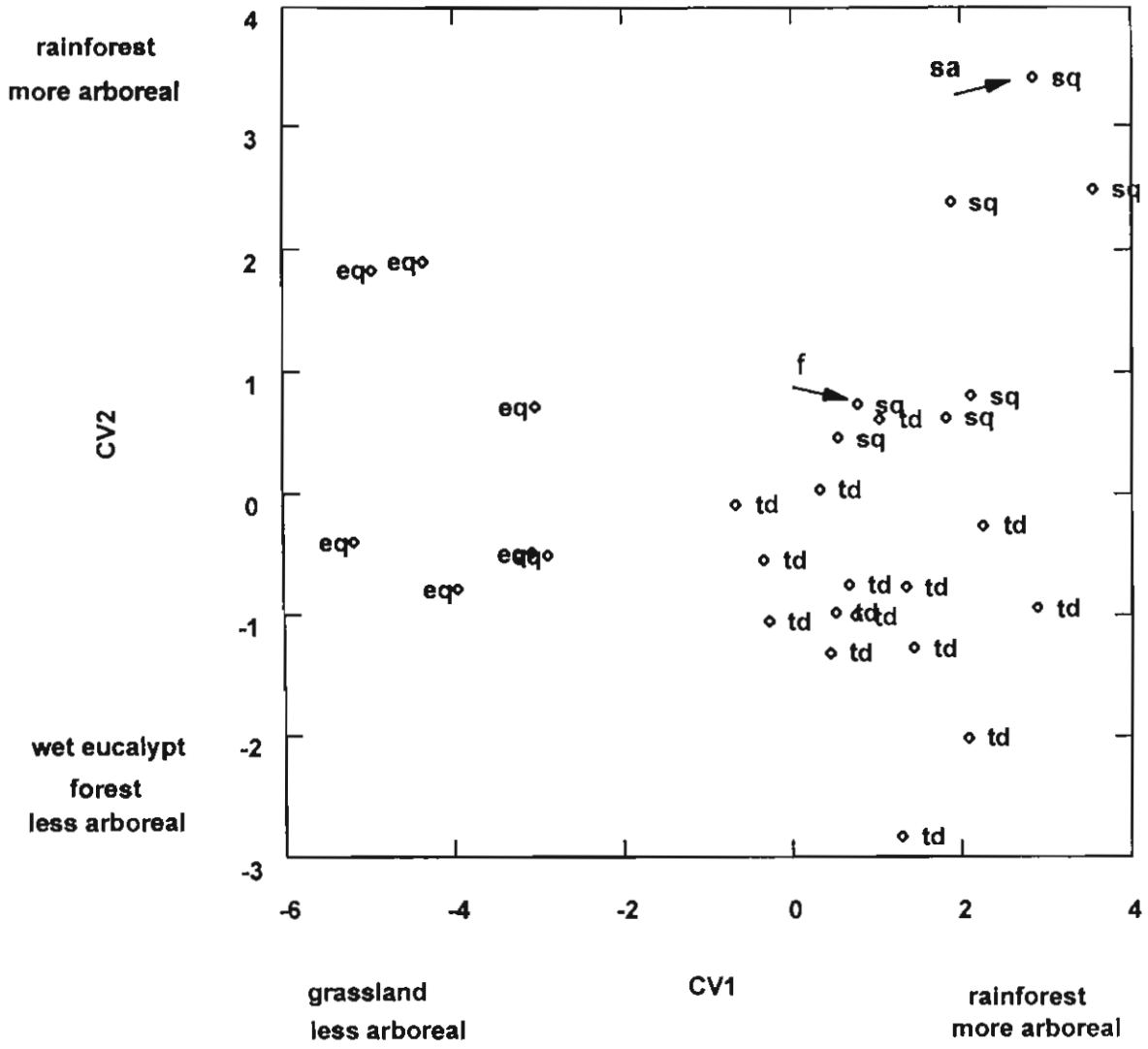


Figure 4.2 Canonical variate plot of habitat use by devils, spotted-tailed quolls and eastern quolls. td = devil, sq = spotted-tailed quoll, eq = eastern quoll, f = female, sa = sub-adult

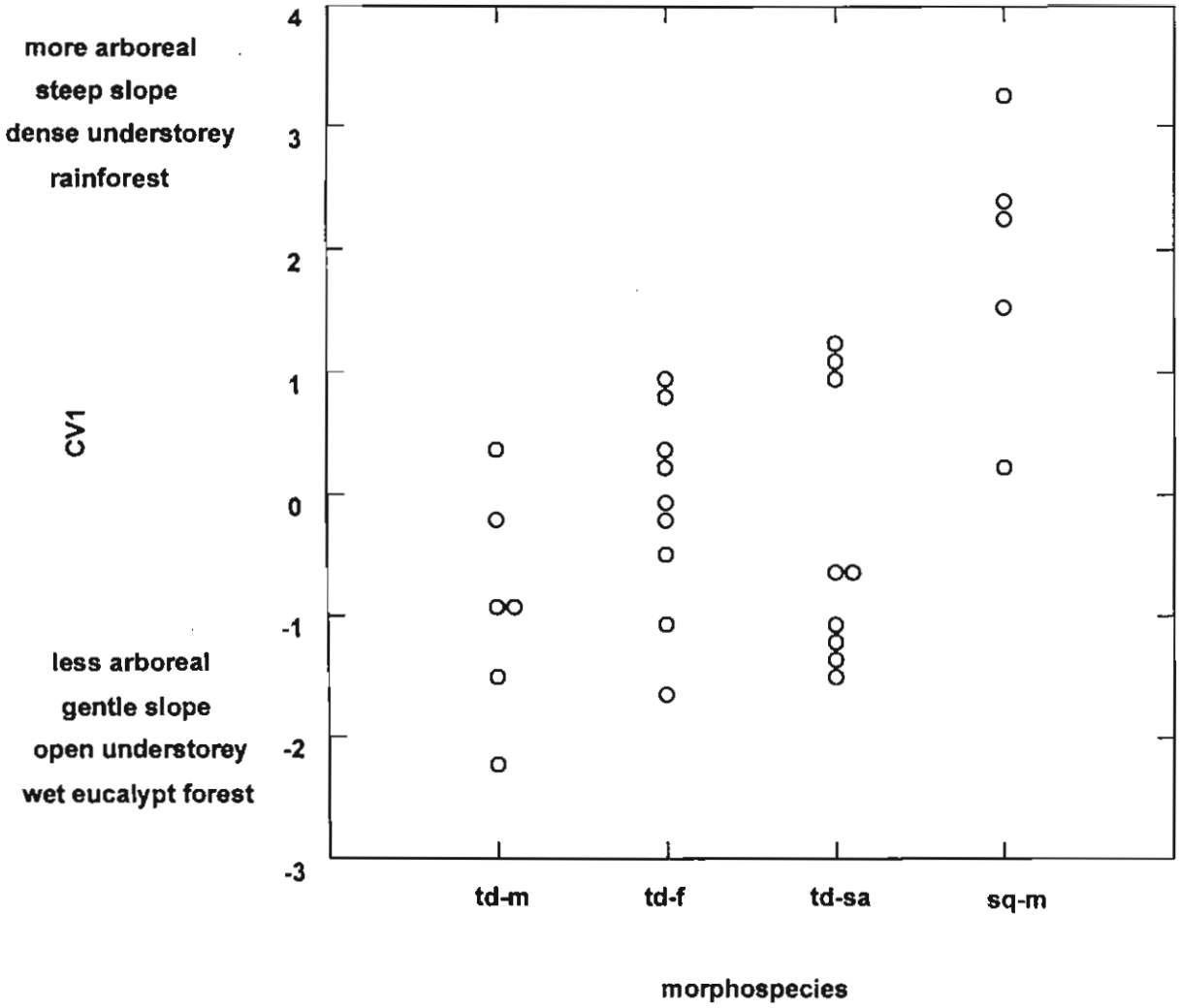


Figure 4.3 Canonical variate plot of habitat use by different age/sex classes of devils and male spotted-tailed quolls. td = devil, sq = spotted-tailed quoll, m = male, f = female, sa = sub-adult

larger sample sizes had been obtained. The small number of sample sizes is a result of the small number of individuals in some species and population classes in the study area.

There is a trend of increasing arboreal activity with decreasing body size in devils. Sub-adults are more arboreal than adult females which are more arboreal than adult males. However, all devils, including sub-adults which have a similar body weight to male spotted-tailed quolls, are less arboreal than male spotted-tailed quolls. The trend of increasing arboreal activity correlates with steeper slopes, denser understorey and more time spent in rainforest. (*Table 4.2* and *Figure 4.3*)

Not enough female or sub-adult spotted-tailed quolls were trapped to enable a similar analysis for the spotted-tailed quoll/eastern quoll body weight overlap to be carried out. The one sub-adult spotted-tailed quoll in the data set (which is of the same body weight range as male eastern quolls) is the most extreme value of the spotted-tailed quolls on CV2 axis (marked with an arrow in *Figure 4.2*). This indicates little overlap in habitat use between spotted-tailed quolls and eastern quolls of a similar body size.

Table 4.2 Percent of total length of spool, and percent of records where the spool was in a foraging pattern, in each habitat type, visibility at half a metre above the ground, steepness of slope, number of logs encountered in habitat and degree of arboreal activity for adult male, adult female and sub-adult devils, and adult male spotted-tailed quolls (mean values for the raw data).

	adult male devil	adult female devil	sub-adult devil	adult male spotted-tailed quoll
% distance in:				
rainforest	12	41	31	53
wet eucalypt forest	58	27	42	3
dry eucalypt forest	12	14	7	12
mixed forest	9	12	12	20
grassland	10	6	7	17
buttongrass	0.3	0	0.1	0
% foraging records in:				
rainforest	10	41	27	37
wet eucalypt forest	52	22	43	3
dry eucalypt forest	13	15	7	45
mixed forest	13	12	14	10
grassland	9	10	8	2
buttongrass	0.3	0	1	2
visibility at 0.5m height	0.78	0.45	0.5	1.3
slope	1.25	1.35	1.31	1.77
no. trees climbed/km	0.15	0.18	0.28	0.42
no. logs encountered/km	6.49	12.9	9.81	14.52
% logs climbed	24	41	43	68
% distance arboreal	0.2	1	1	7
N	6	9	9	5

No species or population class is concentrating its foraging activities near the forest/grassland ecotone. Most activity is well within either forest or grassland. (*Table 4.3*)

Table 4.3 Percent of total length of spool where animal was near a forest ecotone, for devils, spotted-tailed quolls and eastern quolls. Records are separated into those when the animal was in the forest but close to the border with an open habitat, and those where the animal was in the open near the edge of a forest. Forests include rainforests, mixed forests and wet and dry eucalypt forests. Open habitat includes grassland, buttongrass moorland and coral fern.

	devil - mean (range, sd)	spotted-tailed quoll - mean (range, sd)	eastern quoll - mean (range, sd)
percent distance in forest but <15m from open habitat	8.8 (0-46, 12.5)	17.2 (0-41.2, 15.3)	6.3 (0-12.8, 4.4)
percent distance in open habitat but <15m from forest	4.9 (0-16, 6.0)	6.1 (0-15.1, 6.5)	18.0 (0-42.6, 14.9)
N	15	7	7

4.3.2 Arboreal activity, diet and adaptations

There is a correlation between degree of arboreal activity and inclusion of arboreal prey species in the diet but it is not very strong (Pearson correlation coefficient, r=0.49) (*Table 4.4*). Female spotted-tailed quolls have the highest proportion of arboreal prey species in their diet, comprising mostly birds. Sub-adult devils have the second highest percentage of arboreal species in their diet, comprising mostly possums. There is a surprisingly small amount of arboreal prey in the diet of male spotted-tailed quolls, but it is more than adult devils. Their diet comprises more possums and fewer birds than the smaller carnivores. Eastern quolls, which do not spend much time above the ground, have only a slightly smaller percentage of arboreal species in the diet than sub-adult devils but this is primarily birds.

Tests on climbing ability of devils using hair tubes and examination of trees climbed by devils carrying spool-and-line tracking devices indicated that devils are capable of climbing vertical tree trunks to a height of two and a half metres provided the diameter of the trunk does not exceed twenty centimetres. They retreat by jumping down rather than climbing. Devils can climb large trunks only if the angle of recline is less than sixty degrees. Fallen trees which rest on other trees and are not steep and small trees with many small branches may be climbed to a vertical height of four or five metres. In these last two situations, devils climbed back down. Direct observation showed that small sub-adult devils are quite agile climbers. They are

recorded as taking birds at roost (Guiler, 1983). No direct observations were made for adult devils. While both front and hind feet of devils rotate inwards which facilitates climbing (more cat-like than dog-like), devils lack any specialised climbing adaptations (see below and *Figure 4.4*). Their claws, while sharp, are not recurved and their fleshy foot pads are not particularly adapted for climbing.

Table 4.4 Percent biomass of arboreal species, included in the medium and small mammal categories of the dietary analysis (see Chapter 3), constituting the diet of different age/sex classes of devils, spotted-tailed quolls and eastern quolls. Both sexes are combined for devils and eastern quolls because there are no significant differences in diet.

Percent biomass	adult devil	sub-adult devil	male spotted-tailed quoll	female spotted-tailed quoll	adult eastern quoll
medium mammal					
pademelon	19	15	20	0	<1
brush-tailed possum	6	13	5	15	6
ringtail possum	9	13	14	0	5
small mammal					
sugar glider	<1	<1	0	0	1
swamp rat	<1	0	0	0	1
long-tailed mouse	<1	<1	9	19	11
Antechinus spp.	<1	<1	1	10	2
large birds	1	1	3	15	8
small birds	<1	12	7	22	16
Total arboreal mammals	15	26	19	15	11
Total birds	2	13	10	37	24
Total arboreal species	17	39	29	52	35

Spotted-tailed quolls carrying spool-and-line tracking devices climbed up to seven metres up large, near vertical trees with no lower branches. Observations have been made of spotted-tailed quolls stalking and catching birds at roost in large eucalypt trees (Annemarie Watt, pers. comm., 1993) and climbing forwards (like a possum not a cat) down a tree with a small ring-tail possum in the mouth (Phil Bell, pers.comm., 1993). These observations show that spotted-tailed quolls are adept at climbing and predating in trees and are supported by morphological evidence that indicates climbing adaptations. Spotted-tailed quolls have an opposable, clawless hallux, recurved (but not retractable) claws and ridges on the not so fleshy pads of all the feet, very similar to the feet of possums. These structures are lacking on the feet of both devils and eastern quolls. (*Figure 4.4*)

Eastern quolls were recorded scrambling over low fallen timber but not climbing trees. They are capable of balancing on limbs but are not agile climbers (personal observations).

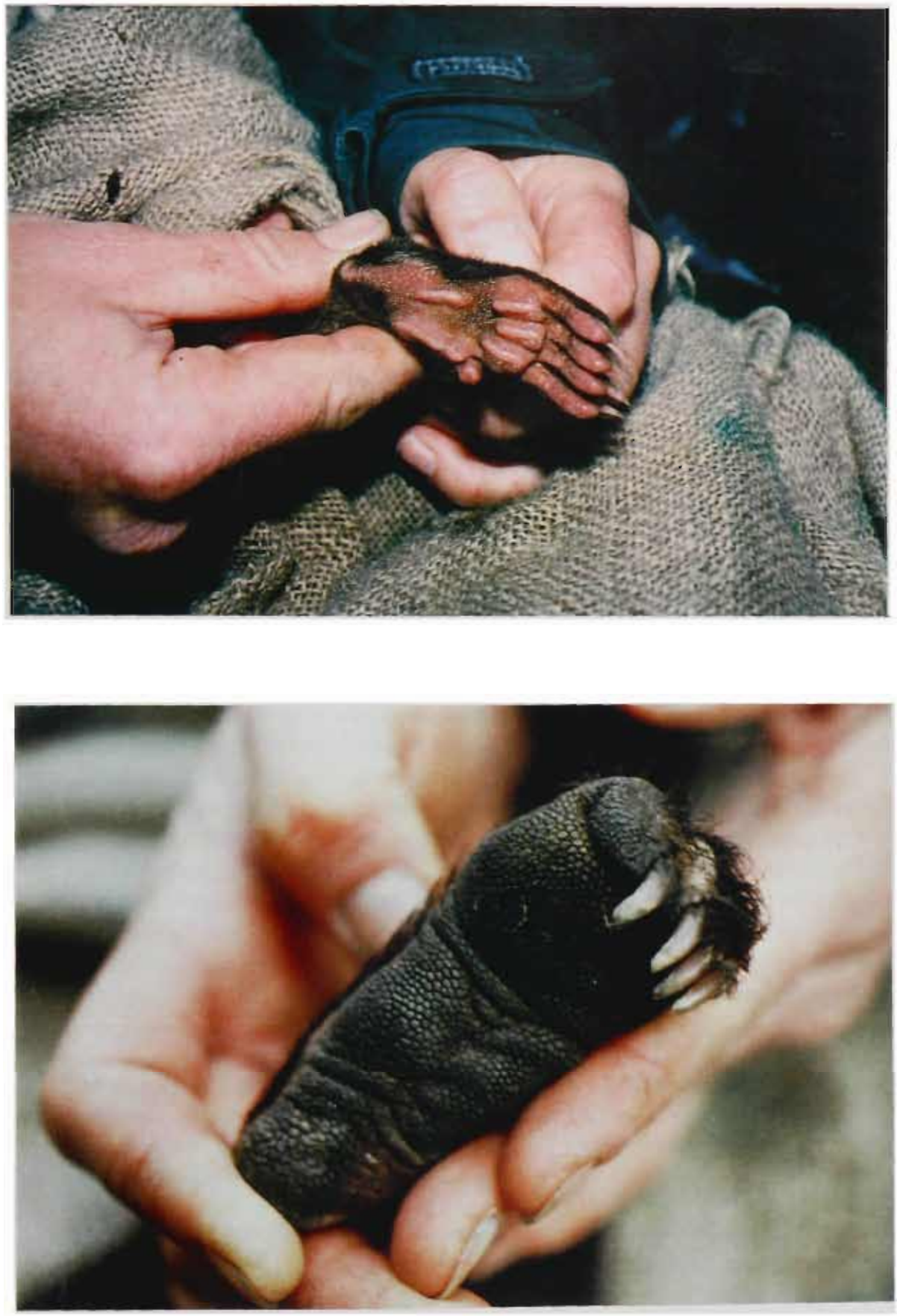


Figure 4.4 Pes of spotted-tailed quoll (above) showing the hallux and ridges on the pads, both adaptations for climbing, and devil (below) demonstrating the lack of climbing adaptations (Photos: Gordon Grigg).

4.4 Discussion

Habitat partitioning is occurring in the guild of marsupial carnivores at Cradle Mountain in addition to partitioning of the food resource. The three species separate out on both horizontal (vegetation type) and vertical (arboreal) use of the habitat. This agrees with the conclusions from Schoener's (1974; 1986) reviews, that resource partitioning in animals usually occurs on two or three (in this case three) niche dimensions. It is impossible to assess whether habitat or food is more important in reducing competition between species.

There is evidence that where morphospecies are similar on one dimension, food, they differ on another, habitat use. This is more evident between female spotted-tailed quolls and eastern quolls than between devils and male spotted-tailed quolls. Within the dietary group comprising all eastern quolls and juvenile and female spotted-tailed quolls, where there is a high degree of overlap in diet and some overlap in body weight, analyses could not be carried out because sample sizes for spotted-tailed quolls were too small. However, the positions of the one female and one sub-adult spotted-tailed quolls that were sampled, on the canonical variate graph indicate that habitat use, both on a horizontal and vertical scale, differs markedly between eastern quolls and female and young spotted-tailed quolls (*Figure 4.2*). Eastern quolls are very much terrestrial, open grassland animals and spotted-tailed quolls are quite arboreal, forest-dwelling animals.

Where there is overlap in diet between age/sex classes of devils and spotted-tailed quolls at certain times of year (Chapter 3), there is also some overlap in habitat use. Adult devils significantly overlapped in diet with adult male spotted-tailed quolls in late winter/early spring ("lean" time of year) and adult male spotted-tailed quolls overlapped in diet with juvenile and sub-adult devils during the remainder of the year (Chapter 3). Differences in habitat type are visible between spotted-tailed quolls and devils but were not significant. This may be due in part to small sample sizes. Both species use all forest types, but spotted-tailed quolls have a (non-significant) bias towards rainforest and devils have a (non-significant) bias towards wet eucalypt forest. However, some overlap in horizontal use of habitat or vegetation type was found.

These marked differences in spatial use of the habitat both between eastern and spotted-tailed quolls and between spotted-tailed quolls and devils, where there are significant overlaps in diet (meaning prey species), would function to reduce direct competition for the same individual prey items.

It is in the vertical use of habitat, or extent of arboreal activity, that there is an interesting parallel between dietary and habitat niche dimensions of devils and spotted-tailed quolls. As body size of devils increases, from sub-adults to adult females to fully grown adult males, the extent of arboreal activity and the proportion of arboreal species in the diet decreases. Male spotted-tailed quolls are quite arboreal and a large proportion of their diet constitutes arboreal prey species. Thus there is a decrease in overlap in both diet and vertical habitat use between devils of increasing size and age classes and male spotted-tailed quolls. Similar to the pattern of dietary

overlap, sub-adult devils, which are the same body weight as adult male spotted-tailed quolls, are intermediate between devils and male spotted-tailed quolls in arboreal activity. In other words, although they are the same size as male spotted-tailed quolls, they are more like devils in their diet and habitat use.

There is a strong relationship between morphological adaptations, prey type and habitat use. Spotted-tailed quolls are very competent and agile climbers, have a number of morphological adaptations specialised for climbing and a reasonably high proportion of arboreal prey species in the diet. Devils (and also eastern quolls) lack any special arboreal adaptations, their climbing abilities are limited and the proportion of arboreal mammal species in the diet is lower. Arboreal mammal species comprised most of the medium-sized mammals. Most large and small mammals, with the exception of the sugar glider and pygmy possums, are terrestrial. The medium-sized species, the spotted-tailed quoll, takes medium-sized prey, most of which are arboreal. This is the only species, therefore, to have evolved arboreal adaptations.

This begs the question as to where the arboreal prey species were being caught, on the ground or off the ground in trees, bushes or on logs. Spotted-tailed quolls have been observed hunting and capturing both possums and birds up trees. Sub-adult devils have been recorded taking birds from the roost. No records exist of eastern quolls or adult devils hunting or capturing prey off the ground. It is unlikely, however, that devils, sub-adult or adult, would be agile enough to pursue a possum up a tree. It was difficult to determine the motive for adult devils climbing trees during the spool-and-line tracking, but in some cases it appeared to be to gain a vantage point. Both brushtail and ringtail possums spend a lot of time on the ground (personal observation; Kristen Hynes, Sarah Munks, pers. comm., 1994) and devils may be ambushing them there. Similarly, small passerine birds often roost and nest in low, dense shrubs, which are common on the forest/grassland ecotone and along streams which flow through open grassland where eastern quolls spend much of their time.

Only a detailed study of prey distribution and movements would elucidate why devils and spotted-tailed quolls occur in the forest types they do. The larger mammal species - wombats, Bennett's wallabies and pademelons - shelter or den primarily in forest but feed to a large extent in open grassland. There was no suggestion that any of the carnivore species concentrated foraging activity on the forest verges, where they could ambush macropods returning to the safety of the forest. On only one spool-and-line tracking sample did an animal move along the ecotone for a significant period of time. This was a spotted-tailed quoll which moved about one hundred metres along the forest verge just inside the forest edge. The highest values for percent activity within fifteen metres of the forest verge are for spotted-tailed quolls and eastern quolls, both near twenty percent (*Table 4.3*). As mentioned above, with eastern quolls, this may be where many birds are captured. Although devils and especially spotted-tailed quolls are sometimes active during the day, there was no evidence for regular crepuscular activity in any of the three species where day active birds may be hunted (Chapter 3; Jones, Grigg & Beard, manuscript). It is also difficult to explain why eastern quolls concentrate their activities in grassland. Small mammals, which comprise the largest dietary category, are reported to have higher

densities in forest, especially wet eucalypt forest in Tasmania (Fox, 1985; Rose, R.K., unpublished). Skinks are the only major dietary item which is expected to be more abundant in open country.

4.5 Conclusions

In conclusion, resource partitioning is occurring on at least three niche dimensions - diet, vegetation type and vertical use of the habitat. Where overlap between species is high on one dimension such as food, another niche dimension is partitioned, as predicted by Schoener (1986). Where high diet overlap occurs between eastern quolls and spotted-tailed quolls, habitat use on both a horizontal and vertical scale is very different. This also occurs between devils and spotted-tailed quolls but it is not so clear. Differences in vegetation or habitat type are visible between spotted-tailed quolls and devils, although with small sample sizes the results are not significant. An interesting parallel in the extent of overlap in diet and vertical use of habitat occurs, however, between spotted-tailed quolls and devils. The decreasing extent of diet overlap that occurs between male spotted-tailed quolls, which are the same body weight as sub-adult devils, and increasing size (and age) classes of devils is paralleled by the extent of overlap in vertical use of the habitat, arboreal activity. Male spotted-tailed quolls are quite arboreal. The extent of arboreal activity in devils decreases with increasing body size. There is a correlation between vertical use of the habitat, percent of arboreal species in the diet and morphological adaptations for climbing. At least vertical use of the habitat is under morphological constraint and represents niche partitioning on an evolutionary scale. The partitioning of horizontal habitat may, on an ecological scale, serve to reduce the overlap in food resource use and thus competition between the three species of carnivores.

Chapter 5 Contests over carcasses: the effect of body size and age of carnivores

5.1 Introduction

Competition can operate by exploitation, the depletion of resources, or by interference, where animals interact directly, one preventing another from using resources. In mobile animals, interference competition takes the form of contests over real resources such as food or over 'surrogate' resources such as a territory, which provides access to the food resources.(Begon, Harper & Townsend, 1990)

Interference both between and within species of the large marsupial carnivores in Tasmania is most likely to occur over large food items. As none of the species are territorial and they are all solitary with overlapping home ranges (devil, Pemberton, 1990; eastern quoll, Godsell, 1983b) and by extrapolation supported by trapping records from this study the spotted-tailed quoll), interactions between species and possibly within species of devils and quolls are likely to be limited to feeding congregations at carcasses, the mating period and mother/young relationships (Pemberton & Renouf, 1993). Most prey consumed by eastern quolls and female spotted-tailed quolls, and a smaller proportion of the prey consumed by male spotted-tailed quolls and devils are small enough in relation to the body size of the carnivore to be consumed entirely in a relatively short space of time (Chapter 3). Thus the opportunity for the food itself to be the subject of contest and perhaps taken over by another animal is small. A significant proportion of the diet of devils and male spotted-tailed quolls, however, consists of prey species that are much larger than the predator and much larger than can be consumed in one meal. A keen sense of smell, dense populations of devils and secondarily of eastern quolls, and the very vocal communal feeding of devils (Pemberton, 1990; Pemberton & Renouf, 1993), make it likely that large carcasses, whether killed by the possessor or scavenged, will be found by other carnivores, both of other species and conspecifics. It is over large carcasses that direct contests over food resources are most likely.

The aim of this chapter is to determine the dominance relations between and within species and the resultant extent of scavenging by each of the three species of marsupial carnivores. This will be achieved by examining interference competition over large, scavenged food resources, the carcasses of large prey species. The following questions will be addressed. Which species or population classes within species gain the most feeding time? What factors determine the outcome of contests? What is the nature of the interactions? And finally, are there differences in vigilance behaviour between species or population classes and what factors correlate with these differences? Although staking out carcasses artificially attracts animals to an area to feed, carcasses of the species used in this study do occur naturally in the study area. The results can be interpreted as representing the natural behaviour of the carnivore species.

5.2 Methods

5.2.1 Observations at carcasses

Feeding interactions and behaviour of the large marsupial carnivores at Cradle Mountain were investigated by staking out carcasses of large prey species and observing the activities of animals that were attracted to feed. While spotted-tailed quolls and devils are occasionally observed during the day, and young devils often become active at dusk, the three species are really nocturnal, so after initial trials of daylight observation, all carcasses were observed during darkness.

Carcasses of road-killed animals, usually wombats or Bennett's wallabies (*Macropus rufogriseus rufogriseus*) in excess of 20 kg, that had been killed on Tasmanian roads were collected. They were firmly tied with tie wire to short metal stakes or logs. Two white lights mounted on a 1.5 metre pole shone onto the carcass from above. Car reversing lights were found to be suitable because they operate on 12 Volt batteries and the plastic light cover ensures a diffuse scatter of light over and around the carcass. Large dasyurids are tolerant of this diffuse overhead lighting but will not tolerate bright lights or lights shining towards them at ground level. The lights were powered by a 12 volt car battery and the brightness controlled using a home-built dimmer switch made in the Zoology Department workshop by Kit Williams. Between five and ten minutes was usually required to habituate newly arrived solitary animals to the full strength of the lights. Devils and even eastern quolls would sometimes try to drag the carcass into the shadows or bushes but, once feeding, animals became tolerant of the lights. Two squabbling devils, intent on eating as fast as possible, were even quite oblivious to the researcher attempting to drag the carcass, which had been broken free, back into the light.

Observations were made from a hide, car or, on a few comfortable nights, from the window of a hut at a distance of fifteen metres. A "surveyor's pole", a half metre long piece of wood, painted alternately black and white at ten centimetre intervals, was placed at the same distance and slightly to one side of the carcass. This aided size ranking of animals and their assignment to population classes. Zeiss 10x40 binoculars facilitated detailed recording of postures.

A total of twenty-nine nights of observation using eighteen carcasses at six different localities were carried out. At seven of the carcasses no animal turned up and on three nights only one devil showed briefly. Data are therefore based on nineteen nights of observation. Observations commenced at dusk and continued until dawn unless the carcass was completely devoured earlier or no animals showed up by 3 am. Night length varied between eight hours in summer and fifteen hours in winter. Each carcass was observed at the same location on successive nights (up to three) until it had all gone. Behavioural observation periods were conducted on alternate months to trapping sessions to avoid contaminating scats collected for dietary analysis. Thus, observations were spread over all seasons. Each locality was only used once per month. All carcasses were placed in the open for ease of observation and varied between one and thirty metres from the forest edge. Sites were selected on the basis of trapping records to maximise the chance of interaction between all three species.

During the observation period, the lights were left off unless there were animals feeding. The carcass was checked with dim lights every two minutes. All arrivals and departures of animals were recorded. Population classes were assigned as adult (large) male, small (female-sized) male, adult female or sub-adult (sexes could not be distinguished), as defined in Section 3.2.2, on the basis of size, as determined by comparison with the "surveyor's pole", and secondary sexual characteristics such as a broad head and neck. Individuals were distinguished by patterns of spots, white patches and scars for each observation period (one to three nights). Individuals were recognised to enable length of feeding time per individual to be recorded.

When animals were present at the carcass, the feeding and vigilance behaviour of each individual was recorded every two minutes. Whether the animal was eating or not was recorded. A feeding bout was defined as all records of an individual feeding separated by less than twenty minutes. A feeding bout was terminated when the animal departed from the carcass for over twenty minutes. Feeding bouts could be continuous or spread over one to one and a half hours with short (less than twenty minute) interruptions. Records when the animal was not feeding were subtracted from the total time the animal was present at the carcass to provide feeding bout lengths. The following vigilance behaviours were identified; posture, whether the animal was rearing on its hind legs, standing, sitting, crouching or lying down; whether it was on the ground or on the carcass; and head position, up or down. Combinations of these postures were combined for analysis into five categories representing increasing vigilance or exaggeration of posture. These are sitting (including lying and crouching), standing or rearing on the ground, and standing or rearing on the carcass. In all these postures defined as vigilant, the animals head was up, a position enabling the individual to survey its surroundings. If its head was down, the individuals' behaviour was recorded as not vigilant.

For all interactions that were visible (a small number occurred in the dark at a distance from the carcass), the species and population class of the animal feeding and the animal attempting to gain access, were recorded and the outcome of the interaction was recorded. Pairs of individuals involved in intraspecific interactions were ranked by size. Three categories of outcomes were assigned, failure of the incoming animal (always the initiator of interactions) to gain access to the carcass, displacement of the feeding animal by the challenger and mutual tolerance where the animals fed together, the challenger gaining access but the feeding animal not being displaced. The behaviours (vocalisations and postures) exhibited during the interaction were briefly identified using the definitions and descriptions of Pemberton (1990; Pemberton & Renouf, 1993).

5.2.2 Analysis of behaviour

The amount of time spent feeding and the nature of the feeding bouts is analysed by species and separately by population class within species, using multivariate analysis of variance and canonical variate analysis. Because of the different time scales of the data, total time spent feeding per night and number of bouts per night are analysed as one data set and bout length, number of interruptions per bout and number of animals on the carcass as another.

While individual animals were recognised for the duration of an observation period (one to three nights) the permanent marking system (ear tattoos) was not visible in the dark so no record was possible of individuals between observation periods. Therefore, the same individuals were sampled a number of times not only within an observation period but probably also on several carcasses. This violates the assumption of independence of data. Because of the small amount of observations, all data had to be used so all statistical results for feeding behaviour should be treated with some caution. Resampling was minimised, however, and the number of different individuals sampled maximised, by locating successive observation periods at opposite ends of the study area, where different individuals lived, and by spanning the observations over two and a half years, whereby the natural turnover of populations would render resampling less likely.

Of all inter- and intraspecific interactions, there were enough data only on intraspecific interactions of devils to analyse statistically. The effect of size and age of animals, sex of adults and the effect of the amount of time both possessor of the carcass and initiator of the interaction had already spent feeding is analysed by multi-way chi-squared and log-linear modelling. The amount of time that the animals involved in the interaction had already spent feeding is divided into three periods for ease of analysis. 0 - 20 minutes = not long, 20 - 45 minutes = an average bout length and more than 45 minutes = the mean total feeding time for a night.

Total amount of time spent in vigilance and the number of vigilance events, in each of the five categories of increasing vigilance, is analysed for species and for population classes within species using multi-way chi-squared analysis and log-linear modelling. In addition, the effect of the number of animals present at a carcass on the vigilance of each sex of devils and eastern quolls is analysed.

5.3 Results

5.3.1 Interspecific interactions

5.3.1.1 Extent of scavenging and temporal nature of feeding bouts at carcasses?

In relation to their relative abundance, devils gain the most feeding or scavenging time of any of the three species. Eastern quolls also commonly scavenge but spotted-tailed quolls were rarely recorded at carcasses in relation to their abundance. (*Table 5.1)* Because there are little data on spotted-tailed quolls, most of the subsequent analysis is on the other two species. Spotted-tailed quolls are only mentioned henceforth where there is enough information. Brushtail possums (*Trichosurus vulpecula*) were observed scavenging on carcasses on three occasions. They did not eat large quantities but were observed nibbling on wallaby ears, intestines and muscle flesh.

Table 5.1 Extent of scavenging by each species. Calculated as cumulative feeding time observed divided by number known to be alive during the study period.

	Total cumulative feeding time observed (min.)	Number alive during study period	Extent of scavenging = Total feeding time / number
eastern quoll	988	49	20.2
spotted-tailed quoll	22	19	1.2
devil	4079	126	32.4

Total feeding time per night per individual does not differ significantly between eastern quolls and devils but the temporal and social nature of feeding bouts does. Devils have fewer but longer feeding bouts than eastern quolls and devils have a larger average feeding group size. There are no differences in the number of interruptions per bout. (*Table 5.2*, *Figure 5.1 a)* and *b)*) Statistical test results are as follows: 1) total feeding time, number of bouts per night data group; MANOVA, Pillai Trace, F=8.434, df=4,176, p=<0.001; Univariate F-tests, df=2,88, total feeding time F=2.891, p=0.061, number of bouts/night F=18.856, p=<0.001; canonical variate scores for factor 1, total feeding time = -0.154, number of bouts/night = 1.061. 2) bout length, number of interruptions , number of animals at carcass data group; MANOVA, Pillai Trace, F=2.776, df=6,330, p=0.012; Univariate F-tests, df=2,166, bout length F=3.705, p=0.027, number of interruptions F=0.485, p=0.617, number at carcass F=6.144, p=0.003; canonical variate scores for factor 1, bout length = -0.541, number of interruptions = -0.101, number at carcass = 0.749. Data for spotted-tailed quolls are included in *Table 5.2* but are too few in number to analyse.

Table 5.2 Amount of time spent feeding, interruptions during feeding and number of conspecifics at a carcass for devils, spotted-tailed quolls and eastern quolls.

	devil		spotted-tailed quoll		eastern quoll	
	N	mean (range, s.d.)	N	mean (range, s.d.)	N	mean (range, s.d.)
length of feeding bout (min)	122	33.35 (0-140, 28.61)	2	11	45	21.96 (1-71, 17.20)
no. interruptions / bout	122	0.66 (0-5, 0.95)	2	0	45	0.67 (0-3, 0.93)
no. conspecifics at carcass	122	1.57 (1-3, 0.69)	2	1	45	1.20 (1-2, 0.41)
no. bouts / night	76	1.63 (1-4, 0.78)	2	1	13	3.46 (1-8, 1.94)
total feeding time / night (min)	76	53.67 (0-225, 39.43)	2	11	13	76.00 (4-148, 50.34)

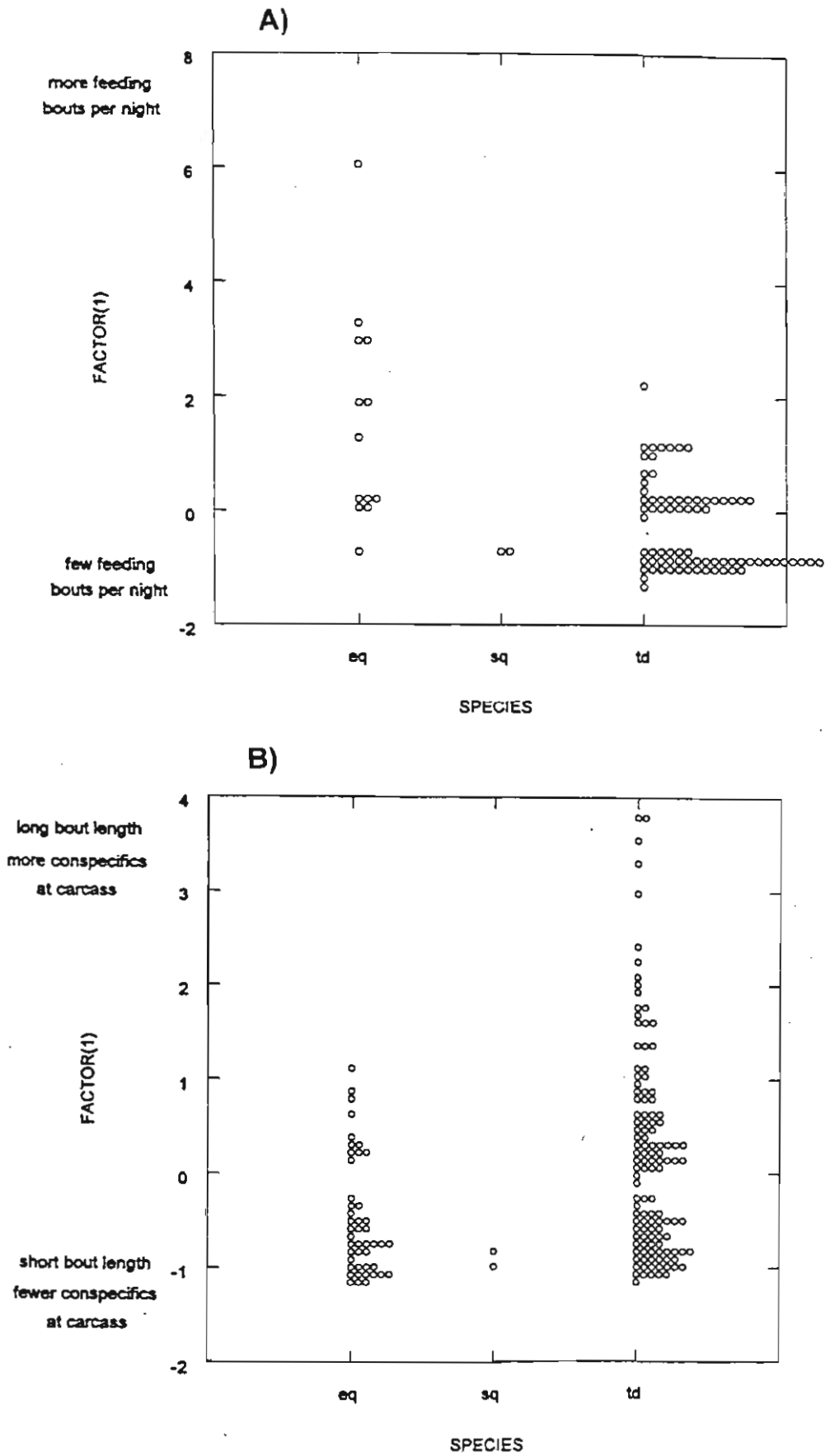


Figure 5.1 Temporal and social nature of feeding in devils, spotted-tailed quolls and eastern quolls. A) Number of feeding bouts per night B) Feeding bout length and number of conspecifics at carcass

5.3.1.2 What are the outcomes of interspecific contests over carcasses?

Interspecific interactions were too few in number for statistical analysis. They are summarised under headings of species pairs.

Eastern quoll / Devil

* In all cases where a devil was in possession of the carcass and an eastern quoll came in close (n=9), the devil remained in possession. In four of these cases, the devil expressed acknowledgment of or irritation at the eastern quoll (stared, snorted, barked, short chase) and the eastern quoll departed rapidly.
* In all cases when an eastern quoll was in possession of the carcass as a devil was approaching (n=10), the eastern quoll became vigilant, often rearing upright on top of the carcass, and departing quickly as the devil came into view, or more commonly, up to a minute before the devil appeared.
* In five cases where a devil had displaced an eastern quoll from a carcass, the eastern quoll returned as the devil was leaving.
* All the above cases (n=24) occurred irrespective of the population class of either the eastern quoll or the devil or whether one or two eastern quolls were present.

In summary, devils always displaced eastern quolls from carcasses but this took the form of avoidance on the part of the eastern quoll which often returned as soon as the devil had finished feeding, leading to a pattern of attendance at a carcass seen over one complete night in *Figure 5.2*. If more than two devils were present, however, the eastern quolls disappeared for the night or came back many hours later.

While eastern quolls were wary of a hungry devil arriving at a carcass, they were not afraid to approach a feeding devil quite closely and fossick around for scraps. Eastern quolls often darted around the carcass and feeding devil, approaching to three metres from the devil and staring at it. In one instance, an eastern quoll made several close approaches, up to two metres behind the devil, culminating in sniffing its' tail. The devil had turned to look at the quoll and had snorted at it a number of times. On the very close approaches, the devil turned and chased the quoll for two to three metres. Being much faster on its feet than the devil, this did not deter the quoll for long. The quoll returned to feed as soon as the devil departed.

In this instance the carcass was still fairly intact and there were no scraps lying around. When a carcass has been nearly completely devoured, particularly if a number of devils have been fighting over it simultaneously, small pieces litter the surrounding ground. On another occasion, when all that was left of the carcass were small scraps of flesh, bone and fur, an eastern quoll and a sub-adult devil fed on these four metres apart, ignoring each other.

Eastern quoll / spotted-tailed quoll

No observations were made.

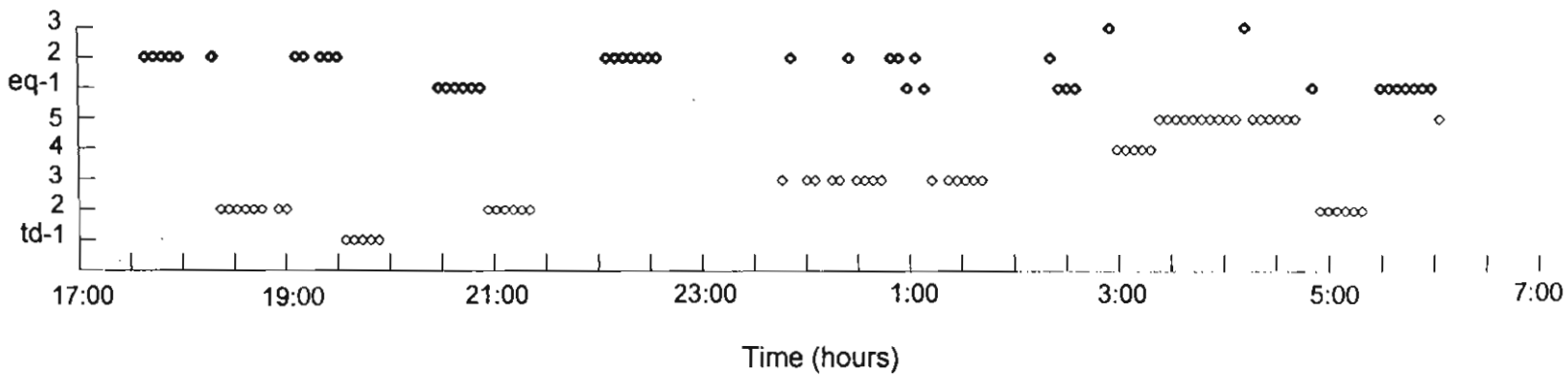


Figure 5.2 Example of presence of carnivores at a carcass, demonstrating the avoidance of devils (= td, 5 individuals) by eastern quolls (= eq, 3 individuals). Data from one night, 6 July 1991.

Spotted-tailed quoll / devil

* Only three interactions were observed.
* An adult male spotted-tailed quoll retreated just before two adult devils came into view.
* One adult female spotted-tailed quoll successfully displaced a sub-adult devil, chasing it fast for fifteen metres.
* One small spotted-tailed quoll (adult female or small male) displaced a sub-adult devil. The devil retreated from the carcass as the spotted-tailed quoll approached.

In summary, age and sex are important as well as body size in determining the outcome of interactions between devils and spotted-tailed quolls. A smaller but older spotted-tailed quoll can displace a young devil.

Brush-tailed possum / eastern quoll

* In only one incident observed, an adult male eastern quoll retreated from a carcass as a brush-tailed possum approached.

Brush-tailed possum / devil

* Two interactions observed
* A brush-tailed possum retreated from a carcass as a devil arrived.
* Two brush-tailed possums retreated up a nearby tree as a devil arrived but came back to the ground fifteen metres away once the devil was feeding.

5.3.2 Intraspecific interactions

5.3.2.1 Which population classes within species gain the most feeding time?

There are no differences among population classes in total time spent feeding, in the temporal nature of feeding bouts or in the number of conspecifics present at the carcass for either devils (MANOVA, Pillai Trace; total feeding time + number bouts per night F=1.686, df=6,138, p=0.129, bout length + number present + number of interruptions F=1.514, df=9,342, p=0.141) or eastern quolls (MANOVA, Pillai Trace; total feeding time + number bouts per night F=0.693, df=2,10, p=0.523, bout length + number present + number of interruptions F=1.184, df=3,41, p=0.328).

5.3.2.2 What are the outcomes of intraspecific contests over carcasses?

Intraspecific interactions among eastern quolls

* Seven interactions were observed, all between an adult male and an adult female.
* In six cases, they shared the carcass, often feeding side by side.
* In four cases, the male chased the female at some stage during feeding, usually on arrival of the female, if the male was in first possession.
* In one case, the female was displaced by an aggressive attack and chase by the male and departed, not returning that night.

In summary, the carcasses were enormous in relation to the size of the eastern quolls and they mostly shared, feeding side by side. Males are larger in body size than females and dominant, males sometimes displacing females but never the reverse. The chasing, however, could have been of a sexual nature rather than relating to competition over food.

Intraspecific interactions among spotted-tailed quolls

No interactions were observed between spotted-tailed quolls and they were only ever seen individually at a carcass. However, they often turned up to feed at the Cradle Mountain Lodge, where dinner scraps were put out for wildlife for the benefit of tourists. On several occasions, two spotted-tailed quolls were present and both were darting in and out picking up small scraps. Only once was an interaction observed. After both had been present for fifteen minutes, a large adult male quoll chased and attacked a small male. The fight, which is best described as a caricature of a dog fight with both animals biting, kicking and rolling on the ground belly to belly, lasted for twenty seconds and resulted in the small male departing. As this fight took place fifteen metres away from the food and was quite intense, it was probably more closely related to intra-sexual dominance than to contests over food.

Intraspecific interactions among devils

Enough intraspecific interactions were recorded for devils to permit statistical analyses. Interactions between six combinations of size and age were observed and analysed. In addition, interactions are analysed between adult males and adult females. There is a significant effect of size and age (Pearson Chi-square = 25.817, df=10, p=0.004), but not of sex (Pearson Chi-square = 3.973, df=6, p=0.680), although sample sizes are very small for this latter analysis.

In devils of the same age, size is a distinct advantage in contests. Larger devils of the same age are less likely to fail to gain access to a carcass and more likely to displace the animal already feeding (*Table 5.3*).

Not enough interactions were observed between devils of the same size but different age (ie. adult females and small males, n = 2) to make generalisations. Of only two interactions, the outcomes went one each way. However, younger, smaller

animals are at a definite disadvantage. They are more likely to fail to gain access and less likely to displace the feeder (*Table 5.3*).

Table 5.3 The effects of size and age of devils on outcome of contests over large carcasses. Data are presented as standardised residuals from log-linear modelling. A residual larger than two indicates a significant effect. The sign of the residual indicates the direction of the effect. (N = sample size, Displaced = initiator of interaction displaced animal already feeding on carcass, Failed = initiator failed to gain access to the carcass, Shared = shared the carcass, initiator gained access and possessor was not displaced)

Size and Age of initiator relative to that of possessor	N	Outcome of interaction		
		Displaced	Failed	Shared
larger - older	41	0.90	-0.80	-0.12
larger - same	18	2.04	-2.38	0.26
equal - same	15	0.89	-1.25	0.31
smaller - older	2	0.41	0.47	-0.84
smaller - same	21	-0.38	0.16	0.22
smaller - younger	59	-2.18	2.43	-0.18

The equal likelihood of initiators that are larger and older than the individual possessing the carcass gaining any outcome (*Table 5.3*) suggests larger, older individuals in a population are more tolerant of and tolerated by the other member of the dyad than same age animals are. This is better understood by examining the population classes making up these dyads. Forty of the forty-one interactions where the initiator was larger and older than the possessor involved an adult and a sub-adult, whereas most of both members of the dyads involved in the larger, same age category of initiator were sub-adults. Sub-adults are generally more active in asserting dominance and are more intense about feeding. This is probably because they are not as efficient or experienced at feeding themselves as adults are, and the dominance relationships between them are in a state of rapid flux. Hence, sub-adults are likely to fight hard to retain possession of a carcass, even if their opposition is adult. Similarly, sub-adults are more likely to displace each other than share a carcass.

A summary of the results by population class produces some interesting results. Large adult males allow females and sub-adults access to the carcass on which they are feeding. They will usually feed together with sub-adults. Females are just as likely to displace males as feed with them. Small males mostly allow sub-adults to feed but are just as likely to be displaced by them as to share the carcass. Adult females usually allow adult males and females to eat, but are more likely to share the carcass only with males. Females are equally likely to share a carcass with other females or to displace the female in possession. Females are less likely to allow sub-adults in to feed at all and are rarely displaced by them. This can probably be

interpreted in terms of recent weaning. Sub-adults don't allow themselves to be displaced by adult males and are more likely to not let them in than feed with them. Sub-adults are displaced by adult females two-thirds of the time but the other third of interactions, they feed with them. Sub-adults are twice more likely to displace each other at a carcass than to feed mutually. They only fail to gain access to the carcass if they are smaller than the sub-adult in possession. Sub-adults initiating an interaction that are larger than those in possession are more likely to displace other sub-adults. Overall, the initiator of an interaction is more likely to gain access than not and the possessor of a carcass is more likely to retain its' possession than not.

The amount of time for which both the initiator of an interaction and the possessor of the carcass had already spent feeding had an effect on the outcome of the contest, although there was no association between feeding time for the initiator and possessor (log-linear model of best fit included main effects and two of the three possible two-way interactions, those between outcome and feeding time of initiator, and between outcome and feeding time of possessor). The possessor of the carcass is most likely to have already fed for an average bout length (20 - 45 minutes) while the initiator of the interaction is most likely to have not fed for very long (< 20 minutes). To summarise trends from the data in *Table 5.4*, both the initiator of an interaction and the devil already in possession of the carcass are more likely to gain access or retain their feeding position at the carcass than not. Displacement of the devil already feeding occurs one third of the time (mean = 33.66) regardless of time spent feeding. The longer a devil has already been feeding for, regardless of whether it is the initiator or possessor, the more likely it is to share the carcass with another devil. (*Table 5.4*)

Table 5.4 Effect of the amount of time that the initiator of the interaction and the possessor of the carcass had already spent feeding on the outcome of the interaction. Note that the three categories of outcomes are not mutually exclusive.

Amount of time already spent feeding by initiator/possessor	N	percent interactions where initiator / possessor gained access / maintained possession	percent interactions where initiator / possessor displaced possessor / was displaced	percent interactions where carcass was shared
init. fed < 20 min.	88	58	32	26
init. fed 20 - 45 min.	20	100	35	65
init. fed > 45 min.	49	67	34	33
poss. fed < 20 min.	52	60	40	23
poss. fed 20-45 min.	63	75	25	32
poss. fed > 45 min.	42	64	36	48

In summary, size, age and sex influence the outcome and intensity of interactions and the degree of tolerance to sharing with other conspecifics. In devils, the possessor of the carcass and the initiator of the interaction are both more likely to retain or gain access than not. Shared feeding becomes more likely as time already

spent feeding increases for both the possessor of the carcass and the initiator of the interaction (the animal attempting to gain access).

5.3.3 Vigilance behaviour

There are no differences in the percentage of time spent in a posture permitting vigilance or in the number of vigilance events between eastern quolls and devils or between population classes within these two species. Statistical results are as follows: 1) for % time spent vigilant: between species t=1.279, df=51.5, p=0.207; between population classes within species, eastern quoll t=1.827, df=29.1, p=0.078 and devil (one-way ANOVA) F=0.156, df=3,84, p=0.925 and 2) for number of vigilance events: between species t=1.279, df=51.5, p=0.207; between population classes within species, eastern quoll t=1.827, df=29.1, p=0.078; devil (one-way ANOVA) F=0.156, df=3,84, p=0.925. (*Tables 5.5, 5.6, 5.7*) Differences between and within species are in the degree of exaggeration of the posture assumed. Results of frequency of postures are the same whether analysed as percent time spent vigilant or number of vigilance events, so only the results for percent time spent vigilant will be presented.

Eastern quolls assume exaggerated vigilance postures (rearing on the ground, standing or rearing on the carcass) much more frequently than expected and relaxed postures (sitting or lying down with head up) much less frequently than expected. Devils are exactly the reverse of this. (Pearson Chi-square = 147.29, df=5, p=<0.001) (*Table 5.5*) Although eastern quolls are much smaller than devils, their head and eyes will still be higher above the ground than that of a devil standing on the ground, when they are rearing on the carcass.

Table 5.5 Percent of time spent in different postures when vigilant for eastern quolls and devils. Data are presented as percent of records in each posture and standardised residuals from log-linear modelling. Standardised residuals greater than two indicate a strongly significant effect, the sign indicates the direction of the effect.

Posture	percent records		standardised residuals	
	eastern quoll	devil	eastern quoll	devil
sitting/lying on ground	9.1	18.6	-3.54	1.79
standing on ground	15.1	14.8	0.14	-0.07
rearing on ground	6.3	<0.1	5.76	-2.92
standing on carcass	5.8	0.0	8.06	-4.09
rearing on carcass	<0.1	0.0	2.49	-1.26
not vigilant	63.2	65.8	-0.48	0.24

There is some but not strong evidence for differences between male and female eastern quolls (Pearson Chi-square = 11.91, df=5, p=0.036). Males assume less vigilant postures than females, with a higher proportion of records than expected

standing on the ground. Females spend more time than expected standing on the carcass and less time than expected sitting, lying or standing on the ground. (*Table 5.6*)

Table 5.6 Percent of time spent in different postures when vigilant for different population classes of eastern quolls. Data are presented as percent of records in each posture and standardised residuals from log-linear modelling. Standardised residuals greater than two indicate a strongly significant effect, the sign indicates the direction of the effect.

Posture	percent records		standardised residuals	
	male	female	male	female
sitting/lying on ground	10.7	6.4	0.82	-1.04
standing on ground	19.2	8.6	1.57	-1.99
rearing on ground	5.4	7.9	-0.57	0.72
standing on carcass	4.5	7.9	-0.81	1.03
rearing on carcass	<0.1	<0.1	-0.21	0.26
not vigilant	59.8	68.6	-0.63	0.80

There are major differences in the frequency of different types of vigilance postures assumed by different population classes of devils (Pearson Chi-square = 89.46, df=9, p=<0.001). Small males are the only age/sex class that spend more time vigilant than expected and they are more likely to stand, a more vigilant posture, than to sit or lie down. This is consistent with small males being more vigilant than other population classes. Sub-adults are the only class of devils in which individuals reared on their hind legs. Adult females are the only class more likely to sit or lie down, less vigilant postures, than stand. No devils were recorded standing or rearing on the carcass. (*Table 5.7*)

Table 5.7 Percent of time spent in different postures when vigilant for different population classes of devils. Data are presented as percent of records in each posture and standardised residuals from log-linear modelling. Standardised residuals greater than two indicate a strongly significant effect, the sign indicates the direction of the effect.

	percent records				standardised residuals			
	male	female	small male	sub-adult	male	female	small male	sub-adult
sitting/lying on ground	17.6	25.3	13.1	15.0	-0.34	3.34	-1.32	-2.11
standing on ground	13.2	10.6	39.3	14.2	-0.59	-2.34	6.59	-0.37
rearing on ground	0.0	0.0	0.0	2.0	-1.37	-2.06	-0.99	2.93
not vigilant	69.3	64.1	47.7	68.8	0.62	-0.43	-2.31	0.95

In summary, percent of total time spent vigilant does not differ significantly between eastern quolls and devils, or between population classes within eastern quolls. Some differences were found between population classes of devils. However, there are significant variations in the frequency of different postures assumed by vigilant animals. Body size and age determine the degree of exaggeration of posture. Smaller and younger animals, both between and within species, display more vigilant postures which require cessation of feeding. Larger or older (adult as opposed to sub-adult) animals more frequently assume less exaggerated postures which enable them to continue feeding while surveying their surroundings.

5.4 Discussion

5.4.1 Extent of scavenging

Devils scavenge to a much greater extent than eastern or spotted-tailed quolls at Cradle Mountain. Devils are morphologically and physiologically well adapted for scavenging and can be considered specialists. They have very strong teeth and heavy jaws and skull. Compared to other marsupial carnivores the skull is very broad at the maximum width of the zygomatic arch. This accommodates massive temporalis and masseter muscles giving a powerful bite both at the canines, and at the bone-crushing teeth and carnassial blades respectively.

Devils are capable of eating all parts of a carcass including the thick skin of the wombat and all but the heaviest bones. Wombat skulls and the pelvic and leg bones of large prey are usually left behind but may be gnawed on subsequent nights. Devils do not have the specialised bone-crushing premolar that spotted hyaenas (*Crocuta crocuta*) possess (Kruuk, 1972). Unlike the eutherian carnivores, the marsupial carnivores (dasyurids and thylacinids) do not have regional specialisation of the molar row (Butler, 1946). The four molar teeth are morphologically similar with minor variations in the length of carnassial shear and the grinding area. Instead, the second molar, classified as M3 by Archer (1978), and to a lesser extent M2, are used for bone-crushing and are worn to stumps in old animals. This tooth is as robust, in terms of width, as the specialised bone-crushing molar in hyaenas, however. Also like the hyaenids, the geometry of the masticatory apparatus has changed from the non-bone specialist carnivore, so that the molar tooth row is further back towards the condyle than in other carnivores, bringing the specialised bone-crushing teeth into the position of maximal bite force (Greaves, 1983). While the marsupial carnivores lack the differentiated carnassial tooth of the Order Carnivora, the last molar, M5, is in the correct position in the jaw to function as the primary carnassial shear (Werdelin, 1986), although both M4 and M5 have extensive carnassial blades suited to slicing the very dense hide of wombats. The teeth of devils, which have more longitudinal than triangular carnassial edges, are much better adapted for meat-slicing carnivory than either of the two smaller quolls. (The evolution and function of the teeth is discussed more fully in Chapters 2 and 6)

Devil scats contain many sharp bone fragments but are also usually grey in colour, changing to white as they dry. Kruuk (1972) stated that the white powder that makes up most of the scats of spotted hyaenas consist of a calcium compound

identical to the inorganic component of bone. When dropped in concentrated hydrochloric acid (HCl), the white powder in devil scats fizzed, indicating it was a carbonate compound, probably derived from bone. It appears as though devils digest substantial amounts of bone, although the bone fragments they swallow are not digested as completely, as in hyaenas.

That devils are the primary scavengers at Cradle Mountain, in that they scavenge more than the other two species of carnivores when the data are corrected for biomass of each species present, is not surprising. They have the ability to gorge up to forty percent of their body weight in one meal (Pemberton, 1990; Pemberton & Renouf, 1993). Ability to gorge has also been recorded in other carnivores, including the lion (Schaller, 1972) and the spotted hyaena (Kruuk, 1972; Tilson & Hamilton, 1984).

The small eastern quolls are not important scavengers in the ecosystem at Cradle Mountain in terms of the biomass of dead animals they consume. Relative to its abundance, however, the species is a significant scavenger. While eastern quolls are recorded as scavenging larger carcasses when available (Godsell, 1983a), the extent of scavenging found in this study has not previously been recorded. Neither has the time spent feeding. Eastern quolls feed at a carcass for the same total amount of time in a night as devils, although they feed more frequently in shorter feeding bouts than devils, which gorge in one or two bouts. Towards morning, eastern quolls which had been returning to feed throughout the night came to the carcass and fed only for a short time, their stomachs distended and tight. Even then, they never had the grossly bloated appearance of gorged devils. They also lack the morphological and physiological specialisations for scavenging that devils have. While eastern quolls consume the bones of small birds and mammals, they were never observed crunching or gnawing bones of large carcasses and their scats have a dark brown, oily appearance, conspicuously lacking in large bone fragments. Their teeth are better adapted for insectivory than carnivory (discussed fully in Chapter 6) and are quite gracile, not robust as in devils.

The lack of scavenging at large carcasses by spotted-tailed quolls in this study, even when corrected for their low abundance, is somewhat surprising given their ability to chase young devils off. Spotted-tailed quolls, of the three species. are the most likely to scavenge around human camps and tame down to the point of handfeeding, even appropriating the role of a cat in sleeping on sunny windowsills of houses in the bush. Care was taken to site carcasses in areas and situations where all three species were regularly trapped, and although the carcasses had to be sited in the open for observations to be possible, they were usually within ten metres of cover and often within a metre of the forest edge. This could have biased the type of species coming into the carcass towards the open habitat dwelling eastern quolls, although devils, like spotted-tailed quolls, also appear to shun open spaces at Cradle Mountain, foraging exclusively in forest. Also, spotted-tailed quolls turn up regularly to the permanent feeding platform at the Cradle Mountain Lodge, which is in the open. This indicates that while spotted-tailed quolls will scavenge from permanent or regular known food sources such as camps, houses and feeding stations, they do not actively seek incidental carrion during their nightly foraging as devils might do. Of the three species, devils have the broadest snout with the largest volume available for

olfactory tissue for their body size, indicating that the sense of smell, useful for finding carrion, is probably developed best in this species. Although, the dentition of the spotted-tailed quoll indicates a more carnivorous diet than the eastern quoll, spotted-tailed quolls are similar to eastern quolls in lacking any morphological or physiological specialisations for scavenging.

Also surprising was the scavenging behaviour of brush-tailed possums (*Trichosurus vulpecula*). They are known to eat meat if offered (How, 1983) and are rumoured to eat eggs and young birds in nests. They have never been recorded scavenging from large carcasses. Early in the study, carcasses were left out all day and observed. The only other scavenger at Cradle Mountain of any size is the forest raven, *Corvus tasmanicus tasmanicus*. They have specialisations for scavenging such as a heavy bill, keen eyesight and large home ranges (Houston, 1979). While frequenting the carcass during the day, the small amount of food consumed and the temporal separation meant that ravens were unlikely to conflict with the mammalian carnivores. All subsequent carcass work was carried out at night.

In summary, devils may actively seek carrion during their nights foraging, being tempted out of forest where they normally forage by the smell of a carcass. In this sense, they are also behaviourally adapted for specialised scavenging. The sense of smell of hyaenas is legendary detecting food from a long way downwind (Kruuk, 1972). It is assumed that devils also have an excellent sense of smell. In one incident, a young devil was seen running towards a barbecue with snout in the air, from hundreds of metres downwind (Bob Hamilton, pers. comm., 1991). Eastern quolls may more easily find carrion that is in open habitat than spotted-tailed quolls would. Care was taken that carcasses were not placed in predictable places. The same locations were not used more than once every four months. Therefore, I was testing the ability and desire of animals to locate incidental carcasses. There was a bias, however, towards placement of carcasses on the open side of forest/grassland ecotones which could partly explain why spotted-tailed quolls were only infrequently recorded scavenging.

5.4.2 Importance of scavenging

It is difficult to assess the importance of scavenging in the diet of any of the three species of carnivores at Cradle Mountain. The cool climate and the large number of devils rapidly cleaning up carrion means that carcasses rarely accumulate blowfly maggots. Therefore, the presence of maggots can not be used as an index of the proportion of the diet that is scavenged. Maggots and human food remains are found at small frequencies in scats of all three species. In the few instances where naturally occurring carcasses were found, the cause of death appeared to be from starvation combined with severe weather in late winter. These carcasses were hardly touched by carnivores and no signs of a struggle were evident indicating that not all scavenge available is utilised.

The presence of prey species in scats larger than could be killed by the carnivore species is not a reliable indicator either. While no evidence was found in either this or Pemberton's (1990) study of devils killing their prey, observations by other people show that devils are capable of killing prey of at least their own body size (pademelon, Andrew Osborne, pers. comm., 1993) and that they will attack the

largest prey species present in the study area (wombat, Dave Probert, pers. comm., 1993). Devils were observed hunting at Cradle Mountain (pademelon, Leon Barmuta, pers. comm., 1992; wombat, Klaus Toft, pers. comm., 1993). Ewer (1968; 1969) and Eisenberg & Leyhausen (1972) described the killing technique used by captive devils on small prey. Buchman & Guiler (1977) did not confirm these results, concluding that devils are inept at killing. Spotted-tailed quolls are capable of killing prey several times their body weight (pademelon, Marty Laarn, pers. comm., 1990). There are no observations to suggest the maximum size of prey that eastern quolls tackle, although they are known to take on potentially dangerous snakes. An eastern quoll was observed with a dead but still writhing white-lipped snake, (*Drysdalia coronoides*), a small elapid (Tony Conlan, pers. comm., 1992). It could be argued that adult Bennett's wallabies and wombats in the diet of spotted-tailed quolls, and any prey larger than a ringtail possum in an eastern quoll scat must be scavenged, but even these may be under-represented in the diet as assessed by scat analysis. When feeding on large carcasses, both species of quolls tug at large areas of muscle flesh opened up by devils. If the carcass is still intact, they quickly go through an area of delicate skin (the pouch and scrotum are common starting points) and pull pieces out from inside. It appears that they would be able to consume a meal without ingesting much or any fur.

Thus, while all three species scavenge and devils have a number of special adaptations for scavenging, it is almost certain that all the marsupial carnivores, including the devil are primarily predators. The work of Hans Kruuk (1972), and George Schaller (1972) demonstrated that hyaenas, the proverbial scavengers, kill a large proportion of their prey and lions frequently displace hyaenas from hyaena kills. Mammals do not have the necessary adaptations for it to be possible for them to derive their entire diet from scavenging meat. These adaptations, which in the higher, homeothermic vertebrates are possessed only by vultures, are the ability to search large areas from the air and move quickly over long distances to reach the carrion, both before it is consumed by other scavengers and if the food supply is migratory. While mammals do not possess these adaptations, the amount of scavenging they do depends on the amount of "free" food available. Carrion will be eaten in preference to exerting energy on hunting and killing (Houston, 1979). This is evident in the behaviour of devils and eastern quolls at Cradle Mountain (and spotted-tailed quolls elsewhere in Tasmania) of travelling roads at night, quickly locating and dispatching roadkills and frequently getting hit as well (Jones, 1993).

5.4.3 Relationships between species

Relations between the carnivorous species at Cradle Mountain reflect the extent of scavenging by each species. Devils are nearly always the dominant species at carcasses. The only exception to this is if an adult spotted-tailed quoll arrives when there is a lone, sub-adult (young) devil feeding, in which case the spotted-tailed quoll will displace the devil. I heard of one incident at Cradle Mountain where a chicken carcass was thrown out for a hand-reared but otherwise wild, large adult male spotted-tailed quoll. A noisy fight was heard some hours later. The spotted-tailed quoll was found badly mauled and was never seen again, presumably dying of his injuries. A badly bitten, large, sub-adult devil was found hiding nearby. (Pat Wessing, pers. comm., 1994) Otherwise, spotted-tailed quolls are quite wary of

devils and will avoid close encounters. Spotted-tailed quoll fur was found in devil scats but it is unknown whether this was predated or scavenged.

The relationship between eastern quolls and devils resembles that between spotted hyaenas and jackals (Kruuk, 1972). The amount of food an eastern quoll could consume in a night of uninterrupted feeding is insignificant to a devil, so they pose very little threat to the food supply at a large carcass. Also, eastern quolls are relatively few in number compared to devils. Consequently devils are quite tolerant of eastern quolls foraging nearby for scraps but not feeding on the same carcass. Eastern quolls repeatedly approach closely behind a feeding devils, eliciting a response where the devil growls and chases the quoll away for a short distance. Whether this is a frustrated attempt to displace the much larger carnivore is a guess. Eastern quolls are much more wary of devils that have not yet fed and are hungry approaching a carcass and generally disappear long before they arrive at the carcass. Although the amount of time spent vigilant is similar between devils and eastern quolls, more exaggerated postures are used by the smaller eastern quolls. An eastern quoll rearing on its hind legs on a carcass gains a higher vantage than a devil standing on the ground. This indicates a greater degree of vigilance in eastern quolls than devils. Intraguild predation was not observed and it is unknown whether devils would try to kill and eat eastern quolls. The chases of eastern quolls by devils were short and not intense. However, eastern quoll fur was found several times in devil scats and three eastern quoll dens were found with the entrance enlarged by digging to devil size. The solitary striped hyaena, *Hyaena hyaena*, either ignores smaller carnivores or treats them as prey (Kruuk, 1976). Kruuk (1972) reported that spotted hyaenas also gained benefit from the presence of jackals because jackals were better at locating and catching young gazelle fawns, which the hyaenas then stole from them. No interactions of this kind were recorded in this study.

Of some surprise is brushtail possums displacing eastern quolls from carcasses, although the possums are much larger. Brushtail possums appear to be very complacent about devils, both when they encountered them at carcasses and at the Cradle Mountain Lodge feeding platform. Provided the devil is intent on feeding on the carcass it is largely ignored by ground-feeding brushtail possums, although they maintained a five metre distance and stayed near the base of a tree. In the artificial situation of the feeding station, brushtails ignored devils even though possum fur occurs frequently in devil scats. On one occasion, a devil lunged and bit a possum on the face when there was no food within the devil's reach. The possum jumped and shook its head but remained on the ground with other possums. On another occasion, a devil was snapping at possum tails dangling through the slats of the feeding platform. The owners lifted their tails but otherwise kept eating. Possums with young on their back were even observed sniffing a feeding devil's head. Brushtail possums have very sharp claws and teeth and could inflict a lot of damage to a devil before they were killed. In the presence of easy food, a carcass or scraps, it is probably not worth the effort for a devil to kill a brushtail.

In summary, interference competition between species operates mostly by avoidance and devils are the clear winners. Both species of quolls combined probably impact little on the carrion resource consumed by devils, regardless of whether it is killed or scavenged by the devils. Body size, which is also correlated

with exploitative ability to deplete the food supply at a carcass, is the most important determinant of the outcome of interspecific interactions or interference competition over large carrion. However, this relationship is tempered by age if body size is similar, an older spotted-tailed quoll can displace a younger devil. While they will feed for the same amount of time as devils, eastern quolls gain access to a carcass only if devils are present intermittently. Where there is a large difference in body size, both species of quolls avoid close encounters with devils at least until the devil is concentrating on feeding. In most situations devils dominate carcasses. Devils are also by far the most abundant of the three carnivore species at Cradle Mountain and in Tasmania overall (Chapter 3). Highest abundance and greatest contribution to the energy flow in the local ecosystem by the largest species in a local assemblage has been reported across a wide spectrum of animals and plants (Brown & Maurer, 1986). Brown suggested this was because of the physiological advantages of large body size and greater mobility, but also that larger species can competitively dominate resource use. The numerical dominance of the Tasmanian marsupial carnivore guild by devils may relate to their competitive dominance in interspecific contests over food. To test this hypothesis requires detailed information on the importance of carrion in the diet of the three species and manipulative experiments where devils are excluded from carcasses.

5.4.4 Intraspecific contests over carrion

It is suggested that intraspecific competition is often much stronger than interspecific competition (reviewed by MacNally, 1983) and therefore cannot be ignored here. Because the only intraspecific interactions observed between eastern quolls were between adult males and females and these are relatively few in number, and none were observed between spotted-tailed quolls, most of the discussion will be focused on devils. This study extends the work on behavioural interactions of devils at artificially placed food by Pemberton (1990; Pemberton & Renouf, 1993) because the age class and sometimes sex of the individuals is identified. Pemberton distinguished individuals only as large, which means adult male, or other. Identification of population class enables a more detailed picture of intraspecific relationships between devils (and eastern quolls) to be constructed.

Buchman & Guiler (1977) found that captive devils form stable linear dominance relationships and suggested the formation of feeding groups with "truce relationships" in the wild which were closed to outsiders. Finding no evidence that large devils had precedence at carcasses, Pemberton & Renouf (1993) suggested that satiation of the feeder was the most important factor determining the outcome of agonistic displays. This study has shown that satiation of the feeder and of the challenger are both important but that age, sex, size and probably also relationships between specific individuals are significant factors in determining access to a carcass. Overall, challengers to the feeding animal are more likely to gain access to the carcass than not, and the feeder is more likely to remain feeding than be displaced. Willingness to share increases with feeder and contester satiation. Once two or more devils are feeding on a carcass, competition for food is translated as eating as fast as possible rather than ceasing feeding to fight, although there is a continual jostling for positions and screeching. This is similar to hyaenas (Kruuk, 1972). The relationships between adult males and all other devils, between females

and sub-adults, and between sub-adults and other devils reveal a complexity in the social organisation of devils not previously appreciated. A study where individuals are consistently recognised is needed to further elucidate the feeding relations of devils.

The relationships between devils are reflected in those observed between adult male and female eastern quolls, although the data are more limited for this species. Similar to the interspecific results, vigilance postures of different population classes of devils and eastern quolls reflected those found between species. Smaller, younger animals or individuals of a lower social rank, such as small or half-grown males, exhibited more exaggerated vigilance postures, which necessitated a cessation of feeding, or more time spent in vigilant postures. Again, intraspecific predation or cannibalism has not been directly observed, although both devil and eastern quoll scats collected in this study were recorded with large amounts of conspecific fur in them. Whether these were scavenged or killed is not known. Devils have been observed eating roadkills of both devils and eastern quolls before the carcass even had a chance to cool. Cannibalism in devils was recorded by both Guiler (1970) and Green (1967). Green stated his evidence as fur present in scats. Guiler, however, claims that young devils are killed by older devils. Hyaena young are sometimes killed by marauding unrelated adults at a den (Kruuk, 1972). With the lack of paternal care in devils, and the need for the female to leave the cubs at the den to forage, there is ample opportunity for cannibalism of young. Narrow, cub-sized tunnels in maternal devil dens, similar to that recorded for hyaenas (Kruuk, 1972), were found at Cradle Mountain. These would enable the cubs to hide from strange devils and reduce the incidence of cub killing.

5.5 Conclusions

In conclusion, all three species of carnivores at Cradle Mountain scavenge. The devil is the primary scavenger, exhibiting morphological, physiological and behavioural adaptations that are lacking in the two quoll species. Interspecific dominance is influenced mostly by body size, but age can also be significant. Outcomes of intraspecific contests over food are the result of a complex interplay of factors, degree of satiation of both the feeder and the contester, body size, age, sex and probably specific relationships between individuals. Further research needs to be done on the social organisation of the devil at the individual level.

Chapter 6 Composition of the mammalian carnivore assemblages in Australia; a comparative overview

6.1 Introduction

Evolutionary history and the physical environment both have a determining role in the biology of species and the composition of species assemblages that come to occupy geographic regions. Because of their different evolutionary histories, continents make ideal natural experiments to examine the relative importance of these two factors. Australia, in particular, is ideal for such comparisons because it has been isolated from other continents for much of its evolutionary history. (Westoby, 1988)

Up until the last few thousand years the carnivorous marsupials of Australasia have evolved in isolation from the placental carnivores (Heatwole, 1987). Ecological convergence with the main morphological types of placental carnivores appears to have taken place over an evolutionary time scale. The thylacine is superficially like a large canid, the devil a small hyaena and the quolls are viverrid-like. Although there are no felid-like marsupial carnivores in Australia at present, there has been in the recent past. *Thylacoleo*, a leopard-sized partly arboreal diprotodontid, which became extinct during the Pleistocene is thought to have been carnivorous (Clemens, Richardson & Baverstock, 1989). The extant marsupial carnivore fauna of Australia is noted for its paucity of species.

In this chapter I shall compare the composition of the Australian marsupial carnivore fauna with eutherian carnivore faunas on other continents. The aim is to explain differences in diversity of species and eco-morphological (diet/locomotor) types in terms of the relative influences of evolutionary history and physical environmental factors. This necessitates an understanding of the diet and hunting strategy of the thylacine. A second aim of this chapter is to extend existing knowledge of the ecological niche of the thylacine. This will be achieved by examining and comparing morphological indicators of diet and locomotion between the thylacine and the large dasyurids.

There have been several different approaches to the morphometric analysis of mammalian carnivore species. Werdelin (1986), extending Radinsky's work on eutherian carnivores (Radinsky, 1981a; Radinsky, 1981b), compared skull shape and functional morphology of marsupial and eutherian carnivores. Keast (1982) compared locomotor function based on limb proportions in three marsupial and three eutherian carnivores to assess the efficiency of the thylacine as a pursuit carnivore. Other than showing that the thylacine is not as well adapted for pursuit as the wolf, his choice of ecologically equivalent marsupial/eutherian pairs of species for comparison was very superficial. Van Valkenburgh (1985; 1987; 1988b; 1989) has derived a series of dental and skeletal indices based on tooth and bone ratios which she has shown represent the diet, hunting and escape behaviour and to a lesser extent habitat selection of eutherian carnivore species. She has used these to compare the structure of placental carnivore guilds in different environments, at different latitudes on different continents, in terms of dietary, locomotory and hunting types. In this

chapter I will extend Van Valkenburgh's work to include the large dasyuroids, comprising the thylacine and the larger dasyurids, to provide a description of the diet and hunting types of the species comprising the Australian marsupial carnivore fauna.

6.2 Methods

All skulls and skeletons used for measurement in this chapter come from fully-grown adult, wild caught marsupial carnivores (definition of "fully-grown" is in Chapter 2, Methods). These came from private research collections (Scott Burnett, Menna Jones) and from the following Museum collections ; the Tasmanian Museum and Art Gallery in Hobart and the Queen Victoria Museum in Launceston, Tasmania, the Museum of Victoria, Melbourne, the Donald Thomson and the Department of Fisheries and Wildlife Collections housed at the Museum of Victoria, the Australian Museum, Sydney, the Macleay Museum of the University of Sydney, the Queensland Museum, Brisbane, the South Australian Museum, Adelaide. The definitions used to distinguish adults are described in Chapter 2.

6.2.1 Tooth wear and tooth breakage

All skulls were assessed for tooth wear and breakage. In addition, all fully-grown adult animals of all three species at the Cradle Mountain study area were assessed for tooth wear and tooth breakage.

Tooth wear was assessed using the schedule devised by Pemberton (1990) to identify age classes. A similar scheme was derived for the canine teeth. (*Table 6.1*) Wear on the lower molars (averaged across both sides) and all four canine teeth was recorded. This was later summarised into two values, one for the canines and one for the lower molars for each animal. Wear was recorded as slight (= categories 0 and 1), moderate (= categories 2 and 3) or heavy (= categories 4 and 5). Broken and missing teeth were recorded by their specific position.

Table 6.1 Classification of wear characteristics for canine and lower molar teeth. The scale and definitions for the lower molars are from Pemberton (1990)

Category	Canine teeth	Lower molar teeth (Pemberton, 1990)
0	no wear	no wear
1	tip worn	tip worn
2	$^1/_3$ - $^1/_2$ worn, enamel intact	dentine showing
3	$^1/_3$ - $^1/_2$ worn, enamel notched	all cusps worn but still distinguishable
4	worn to stumps	no distinguishable cusps
5	flat and worn to gum	flat and worn to gum

The following questions are examined by Pearson Chi-squared analysis. 1) Is the degree of tooth wear on the canines and molars the same between species and between sexes within species? 2) Is the degree of wear similar on the canines to the molars? 3) Does the frequency of tooth breakage differ between species or between sexes within species? 4) Are the type of teeth that break the same in all species and between sexes within species? 5) Do different types of teeth break more or less frequently than expected given the number of each type in a full set of teeth for each species?

6.2.2 Dental indicators of carnivory

A carnivorous diet requires teeth with long, continuous, shearing blades and little grinding surface. By contrast, numerous sharp shearing crests over a wide area and a crushing capacity are needed to process insects (Archer, 1976; Sanson, 1985). The inclusion of fruit and other plant material in the diet requires crushing or grinding surfaces. Hence, in the dasyurids and thylacinids, increasing carnivory (and decreasing insectivory) is correlated with an increase in the length and the longitudinal orientation of the primary carnassial blade (metacrista), a corresponding decrease in the width of the upper molars and the length of the minor shearing blade (paracrista), a decrease in the crushing (talonid) area of the molar teeth, a corresponding decrease in the height of the talonid compared to the trigonid (shearing part of molar), and a posterior shift in the maximum point of carnassial shear (shearing blade length increases towards posterior) (Archer, 1976).

Three measurements were chosen to describe the degree of carnivory in the large dasyuroids, relative blade length, relative grinding area and the angle of the major shearing blade. Two specimens of each sex were measured. Skulls with very worn teeth were not used.

Relative blade length (Van Valkenburgh, 1989) was measured as the ratio of the combined length of the shearing blades (metacrista) of the last two molars (M4 and M5) over the summed total length of the same teeth. Werdelin (1986) considered M5 to be the carnassial equivalent in dasyurids. However, because the position of the carnassial tooth on the jaw in placental carnivores, relative to the condyle, is intermediate to M4 and M5 in dasyurids and the thylacine (Werdelin, 1986), and because neither M5 or M4 become worn during an animals lifetime, both of the last two molar teeth are considered to be important in shearing meat. Measurements to a precision of 0.01mm were taken with Vernier calipers.

Relative grinding area (Van Valkenburgh, 1989), was calculated as $\sqrt{}$total grinding area of the molars / blade length of M4 + M5. Van Valkenburgh's index (for placental carnivores) was modified for dasyurids as follows. The talonid part of each of the four lower molars was identified as the grinding surface (Archer, 1976; Sanson, 1985) and blade length was summed as above. The area of the talonid was measured by drawing the outline of the occlusal surface (parallel to the lens) on paper, using a drawing attachment on a Wild dissecting microscope, and measuring the area to 0.01mm^2 with Mocha Image Analysis Software.

The angle of the major shearing blade was measured as the angle made between the metacrista and the outer edge of the tooth (a line from the metastylar corner of the

tooth to the stylar cusp B) of the second last upper molar, M4. This was equivalent to measuring the angle to the tooth row of the major shearing blade of the last lower molar, M5. The positions of the cusps were drawn on paper using a drawing attachment as above and the angle measured to 0.5° using a protractor.

The species were separated according to degree of adaptation to carnivory using a multivariate analysis of variance and discriminant function analysis.

6.2.3 Morphological indicators of trophic and locomotor diversity

Morphometric ratios that reflect diet content were measured for comparison of trophic diversity with placental carnivores. Relative premolar size (RPS) is calculated by dividing the maximum width of the second lower molar, M3, by the cube root of body weight. M3 is the tooth that is probably used for bone crushing in devils and is the equivalent of the third lower premolar in hyaenas. (Van Valkenburgh, 1989) uses the largest lower premolar, the third or fourth, of placental carnivores. Relative blade length (RBL) is calculated as above. Two males and two females of each species were measured. Each species is assigned, using information from either the literature or this study, to a dietary group according to Van Valkenburgh (1989) classification. Her four groups are

1. Meat: diet comprised of more than 70% meat
2. Meat/bone: greater than 70% meat with the consumption of large bones
3. Meat/nonvertebrate: 50-70% meat with insects and/or fruit
4. Nonvertebrate/meat: less than 50% meat, insects and fruit predominating

Two skeletal ratios that provide a reasonably accurate description of the hunting, locomotor and encounter behaviour of carnivores are calculated (Van Valkenburgh, 1985; 1987). These are the metacarpal/phalanx (MCP) and femur/metatarsal ratios (FMT). Skeletons of two males and two females of each species were measured. In addition, each species is assigned a locomotor and hunting type according to the classification set up by Van Valkenburgh (1985; 1989). Locomotor types are:

1. arboreal: rarely on ground, forages in trees
2. scansorial: capable of climbing
3. terrestrial: rarely or never climbs; may dig burrow but not for food
4. semifossorial: digs for both food and shelter

Hunting types are:

1. ambush: stalk and rush prey, use forearms to grapple prey
2. pounce/pursuit: a moving search involving either a pounce or short pursuit, no grappling
3. pursuit: long distance chase, no grappling

Trophic and locomotor indices are plotted with log body weight in three dimensional morphospace for comparison with placental carnivores (copied from Van Valkenburgh, 1985; 1989). The variables need to be transformed to standardised normal deviates to compensate for differences in scale (Van Valkenburgh, 1985; 1989). The standardised deviates are calculated using all the data on both placental (Van Valkenburgh, 1985; 1989) and marsupial (this study) carnivores even though the dental indices are not exactly equivalent (Sneath & Sokal, 1973, p. 154).

6.3 Results

6.3.1 Tooth wear and tooth breakage

There are major differences in the degree of tooth wear among species (Pearson Chi-square = 138.27, $df = 25$, $p = <0.001$). Devils have much more tooth wear than other species. Spotted-tailed quolls are intermediate between devils, and the other four species, thylacines, eastern, northern and western quolls, show only slight tooth wear. (*Table 6.2*)

The only species in which the amount of tooth wear differs between the sexes is the spotted-tailed quoll. Males have more wear than females (Pearson Chi-square = 14.84, $df = 5$, $p = 0.01$). The results for the other species are devils (Pearson Chi-square = 7.95, $df = 5$, $p = 0.16$), eastern quolls (Pearson Chi-square = 3.30, $df = 5$, $p = 0.65$) and northern quolls (Pearson Chi-square = 1.90, $df = 3$, $p = 0.59$). There are insufficient data to analyse for thylacines and western quolls. (*Table 6.2*)

In both spotted-tailed quolls and eastern quolls, there are large significant differences in the degree of wear on the canines and molars, the molars showing heavier wear (spotted-tailed quolls Pearson Chi-square = 23.59, $df = 2$, $p = <0.001$; eastern quolls Pearson Chi-square = 9.07, $df = 2$, $p = 0.01$). (*Table 6.2*) There is slightly but significantly heavier wear on the molars of devils than on the canines (Pearson Chi-square = 6.31, $df = 2$, $p = 0.04$). Thylacines and northern quolls have similar amounts of wear on both canines and molars (thylacines Pearson Chi-square = 2.50, $df = 2$, $p = 0.29$; northern quolls Pearson Chi-square = 0.79, $df = 2$, $p = 0.38$).

Table 6.2 Severity of wear on the canine and molar teeth of individuals of all of the species of large Australian marsupial carnivores and differences between the sexes for each species.

Species / Sex	N	Percent in each stage of wear					
		Canines			Molars		
		slight	moderate	heavy	slight	moderate	heavy
thylacine	50	64	34	<1	50	44	6
devil	93	41	44	15	25	52	23
spotted-tailed quoll	157	53	30	17	31	58	11
eastern quoll	145	81	17	1	66	32	1
northern quoll	26	73	27	0	62	38	0
western quoll	4	50	50	0	50	50	0
By sex							
thylacine - male	7	71	29	0	43	43	14
- female	4	50	50	0	50	50	0
devil - male	32	31	52	17	16	47	38
- female	61	47	39	14	30	54	16
spotted-tailed quoll- male	119	49	31	20	24	62	14
- female	38	63	29	9	53	44	3
eastern quoll - male	94	79	19	2	64	34	2
- female	51	86	14	0	70	30	0
northern quoll - male	11	73	27	0	46	55	0
- female	11	64	36	0	73	27	0

Devils and spotted-tailed quolls have much higher rates of tooth breakage than the thylacine or the smaller species of quolls (Pearson Chi-square = 26.41, $df = 8$, $p = 0.001$) (*Table 6.3*). There are no differences in the rate of tooth breakage between males and females for any species (devils Pearson Chi-square = 1.13, $df = 3$, $p = 0.77$; spotted-tailed quolls Pearson Chi-square = 0.28, $df = 3$, $p = 0.96$; eastern quolls Pearson Chi-square = 2.65, $df = 2$, $p = 0.27$). There are insufficient data for thylacines and northern quolls for analysis.

Table 6.3 Frequency of tooth breakage in individuals of all of the species of large Australian marsupial carnivores and differences between the sexes for each species.

Species / Sex	Percent of individuals categorised by number of broken teeth			
	0	1 - 2	3 - 5	> 5
thylacine	52	36	10	2
devil	32	38	14	16
spotted-tailed quoll	35	32	17	17
eastern quoll	61	30	8	0
northern quoll	77	15	8	0
By sex				
thylacine				
- male	0	67	33	0
- female	50	50	0	0
devil				
- male	16	53	16	16
- female	41	30	13	16
spotted-tailed quoll				
- male	27	35	19	19
- female	61	21	11	8
eastern quoll				
- male	56	32	12	0
- female	71	28	2	0
northern quoll				
- male	73	9	18	0
- female	82	18	0	0

There are major differences between species in the type of teeth that are broken (Pearson Chi-square = 90.18, $df = 12$, $p = <0.001$). Devils break incisors more often than other species. The three species of quolls break canines more frequently than devils or thylacines do. Thylacines and spotted-tailed quolls break molars more frequently than other species. (*Table 6.4*)

Differences between sexes are found in tooth breakage patterns in devils (Pearson Chi-square = 16.40, $df = 3$, $p = 0.001$) and spotted-tailed quolls (Pearson Chi-square = 16.49, $df = 3$, $p = 0.001$). Male devils break molars more often, females break more incisors. Male spotted-tailed quolls break more incisors, females more molars. No differences are found between the sexes for eastern quolls. Insufficient data are

available for analysis of gender differences for thylacines and northern quolls. (*Table 6.4*)

Table 6.4 Frequency of different types of teeth broken individuals of all of the species of large Australian marsupial carnivores and differences between the sexes for each species.

Species / Sex	Percent of broken teeth of each tooth type			
	Incisors	Canines	Premolars	Molars
thylacine	36	13	24	27
devil	59	15	15	11
spotted-tailed quoll	26	28	21	26
eastern quoll	31	36	18	16
northern quoll	29	29	29	13
By sex				
thylacine				
- male	0	15	46	39
- female	0	0	100	0
devil				
- male	49	16	16	20
- female	67	14	15	5
spotted-tailed quoll				
- male	28	28	22	22
- female	10	29	14	47
eastern quoll				
- male	30	38	17	15
- female	33	29	19	19
northern quoll				
- male	33	33	18	18
- female	0	0	100	0

Differences in the frequency of different types of teeth that are broken compared to what is expected from the number of each tooth type are found in three out of four species. Devils break incisors and canines much more frequently and premolars and molars much less often than expected (Pearson Chi-square = 23.76, $df = 3$, $p = <0.001$). Spotted-tailed quolls break more canines than expected (Pearson Chi-square = 8.08, $df = 3$, $p = 0.044$). Eastern quolls also break canines much more frequently than expected (Pearson Chi-square = 13.59, $df = 3$, $p = 0.004$). Breakage of different types of teeth is not different from expected for thylacines (Pearson Chi-square = 1.16, $df = 3$, $p = 0.76$). Sample sizes for northern quolls are too small for analysis but the pattern in the other two quolls of high breakage of canines seems to hold. (*Table 6.5*)

Table 6.5 Number of broken teeth of each tooth type divided by the number of teeth present in each animal for all of the species of large Australian marsupial carnivores. If tooth breakage is equally likely for any type of tooth, values for each tooth type will be equal.

	Tooth type			
	Incisors	Canines	Premolars	Molars
Number of broken teeth / Number of teeth present				
thylacine	1.43	1.75	1.08	0.94
devil	10.64	9.25	4.75	1.69
spotted-tailed quoll	7.14	27.25	10.38	6.25
eastern quoll	2.00	8.00	2.00	0.88
northern quoll	0.14	0.50	0.25	0.06
Number of teeth present				
Family Thylacinidae	14	4	12	16
Family Dasyuridae	14	4	8	16

6.3.2 Dental indicators of carnivory

There are strongly significant differences among species in the degree of adaptation to carnivory as measured by dental indices (Pillai Trace = 2.57, $F = 16.82$, $df = 18,51$, $p < 0.001$). Devils have the most carnivorous dentition, with the longest relative blade length, smallest relative grinding area and most longitudinal orientation of the major shearing crest (*Figure 6.1*, *Table 6.6*). Thylacines are distinctly less adapted for carnivory than devils but are more carnivorous than any of the quolls. The four quoll species overlap as a group, although the spotted-tailed quoll is the most carnivorous and the northern quoll the least.

Table 6.6 Summary statistics of dental indices used to describe degree of adaptation to carnivory. Means and standard deviations given. N = 4 for all species except for the western quoll where n = 3.

Species	Relative blade length	Relative grinding area	Angle of shearing blade
Thylacine	0.81±0.01	0.31±0.04	30.00±3.65
Devil	0.89±0.03	0.21±0.02	26.63±2.14
Spotted-tailed quoll	0.78±0.02	0.34±0.01	52.25±2.78
Western quoll	0.75±0.06	0.44±0.03	50.33±7.51
Eastern quoll	0.73±0.03	0.39±0.03	47.50±2.86
Northern quoll	0.73±0.03	0.45±0.02	56.00±2.16

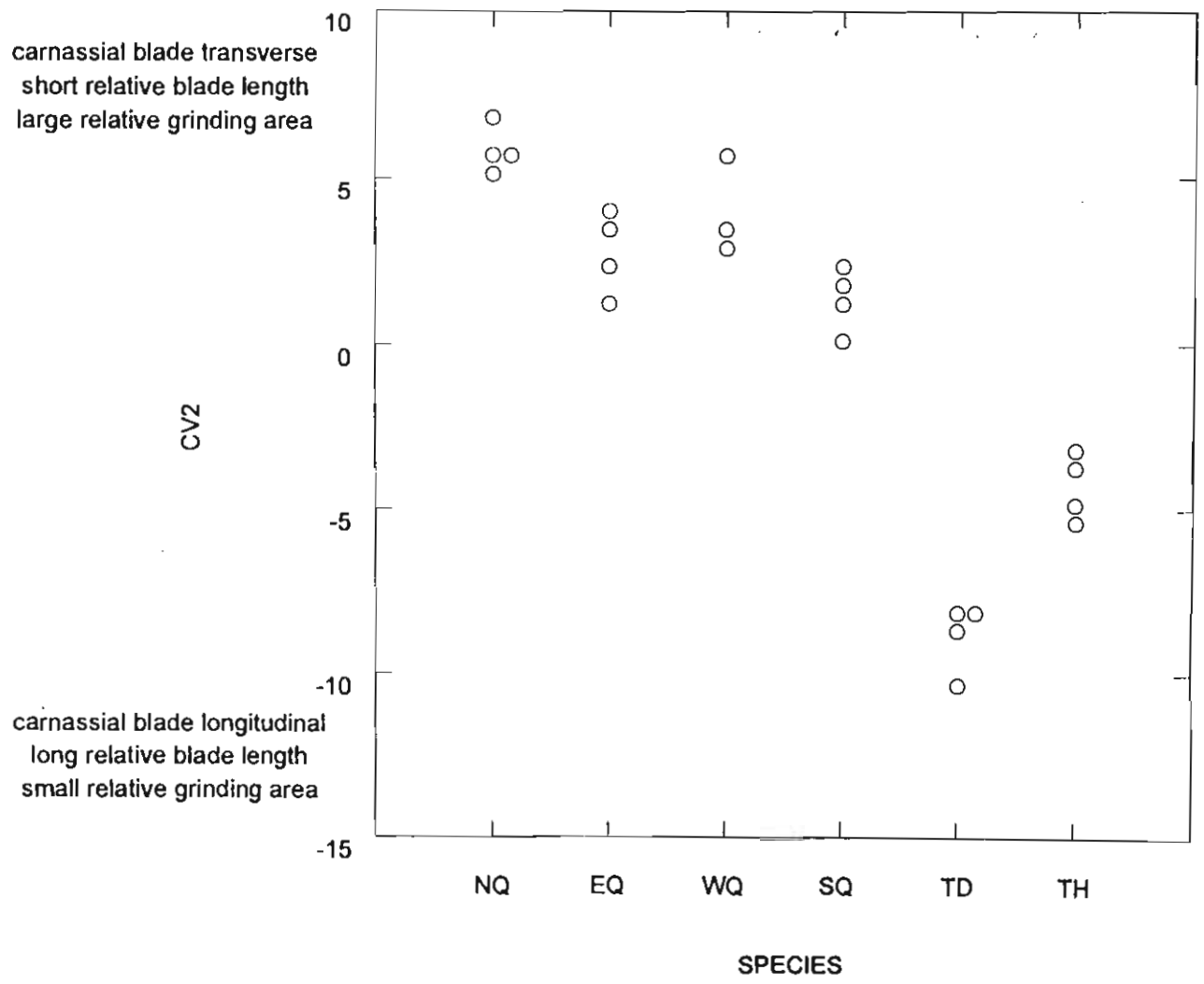


Figure 6.1 Separation of the Australian species of marsupial carnivores by dental indices that indicate degree of carnivory. NQ = northern quoll, EQ – eastern quoll, WQ = western quoll, SQ = spotted-tailed quoll, TD = devil and TH = thylacine

6.3.3 Morphological indicators of trophic and locomotor diversity

Dietary, hunting and locomotory classifications of the marsupial carnivores and the values of the dental and skeletal indices for these species used in comparisons with placental carnivores are in *Tables 6.7* and *6.8*. These are plotted in three dimensional morphospace and placed for comparison alongside (Van Valkenburgh, 1985; 1989) graphs for placental carnivores in *Figures 6.2* and *6.3*.

Table 6.7 Values of the dental indices and dietary classification of marsupial carnivores used for comparison with placental carnivores. Classification and indices according to Van Valkenburgh (1989)

Species	Dietary category	log. body weight (LBW)	relative premolar size (RPS)	relative blade length (RBL)	References for diet and weight
thylacine	meat	1.40	2.14	0.81	(Guiler, 1985; Dixon, 1989)
devil	meat/bone	0.84	3.56	0.89	(This study)
spotted-tailed quoll	meat	0.39	2.84	0.78	(This study)
eastern quoll	meat/nonvertebrate	-0.04	3.23	0.73	(This study)
western quoll	meat/nonvertebrate	0.03	2.65	0.75	(Soderquist & Serena, 1994)
northern quoll	probably meat/nonvertebrate	-0.26	3.04	0.73	(Begg, 1983)

Table 6.8 Values of the skeletal indices and classification by hunting and locomotory type of marsupial carnivores used for comparison with placental carnivores. Classification and indices according to Van Valkenburgh (1985)

Species	Locomotor type	Hunting type	metacarpal/phalanx ratio (MCP)	femur/metatarsal ratio (FMT)	References for locomotor and hunting types
thylacine	terrestrial	pursuit?	2.27	3.31	(Keast, 1982)
devil	terrestrial	pounce/pursuit?	2.36	3.42	(This study)
spotted-tailed quoll	scansorial	ambush?	1.59	3.23	(This study)
eastern quoll	terrestrial	pounce/pursuit	2.02	2.41	(This study)

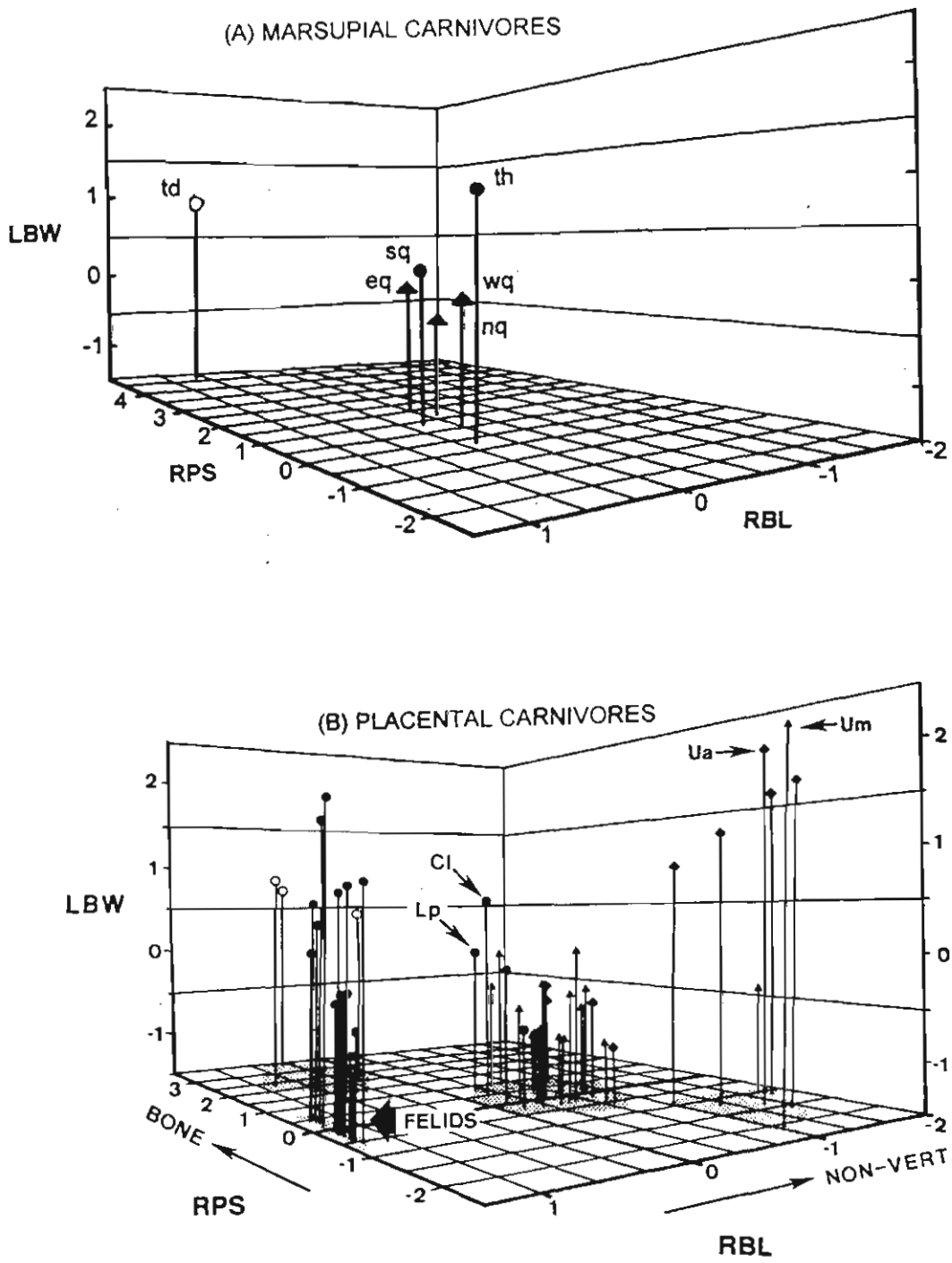
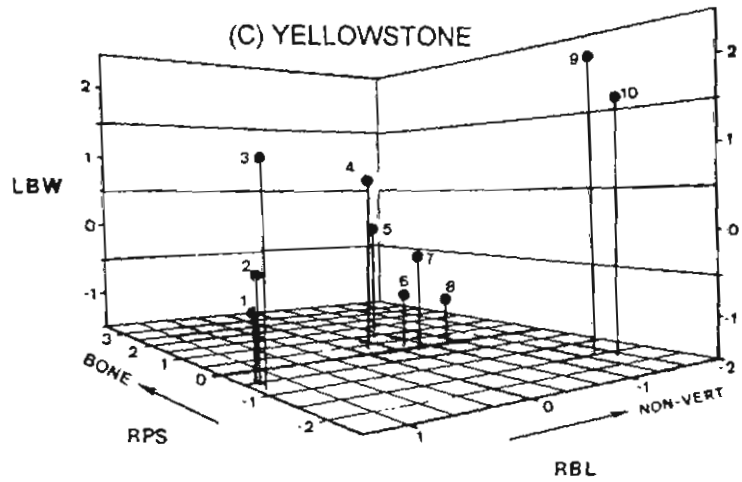
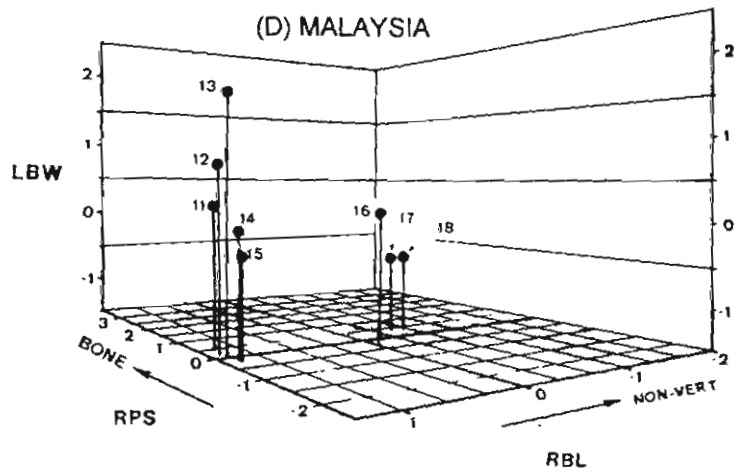
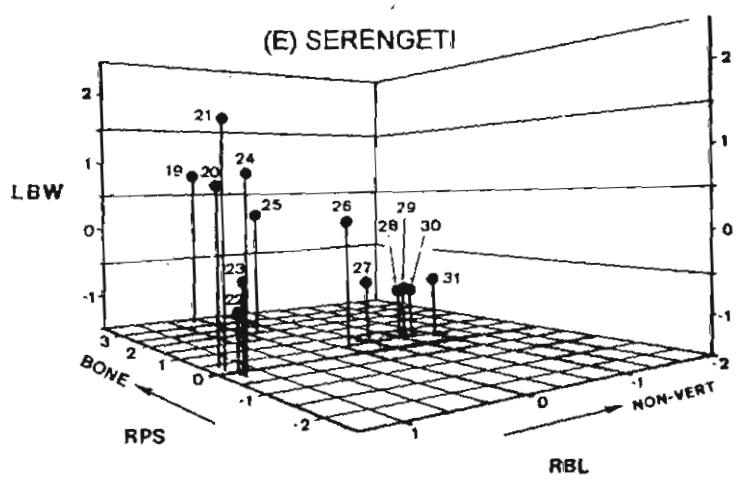


Figure 6.2 Dental morphospace and body size in mammalian carnivores. (A) All large marsupial carnivore species in Australia (for the Tasmanian guild, ignore the western and northern quolls) (B) All placental species (C) Yellowstone, (D) Malaysia, and (E) Serengeti. (B - E) are copied from [Van Valkenburgh, 1989 #55]. Increasing values of relative premolar size (RPS) correlate with an increasing amount of bone in the diet. Decreasing values of relative blade length (RBL) represent an increasing amount of non-vertebrate food in the diet. LBW is log. body weight.
Dietary classifications are as follows: Meat group, solid circles; Meat/bone group, open circles; Meat/nonvertebrate group, triangles; Nonvertebrate/meat group, circles.
Species are as follows: (A) th, thylacine; td, devil; sq, spotted-tailed quoll; eq, eastern quoll; wq, western quoll; nq, northern quoll (B) Lp, African wild dog; Cl, grey wolf; Ua, grizzly bear; Um, polar bear (C - E) 1, bobcat; 2,Canadian lynx; 3, puma; 4, grey wolf; 5, wolverine; 6,red fox; 7,coyote; 8, North American badger; 9,brown bear; 10, American black bear; 11, clouded leopard: 12. leopard; 13, tiger; 14, Temminck's cat; 15, fishing cat; 16, dhole; 17, large spotted civet; 18. binturong; 19, spotted hyaena; 20,leopard; 21, African hunting dog; 27,ratel; 28, side-striped jackal; 29, black-backed jackal; 30, golden jackal; 31, African civet. Placental carnivores (B - E) from (Van Valkenburgh, 1989).


(C) YELLOWSTONE
LBW
BONE
RPS
RBL
NON-VERT


(D) MALAYSIA
LBW
BONE
RPS
RBL
NON-VERT


(E) SERENGETI
LBW
BONE
RPS
RBL
NON-VERT

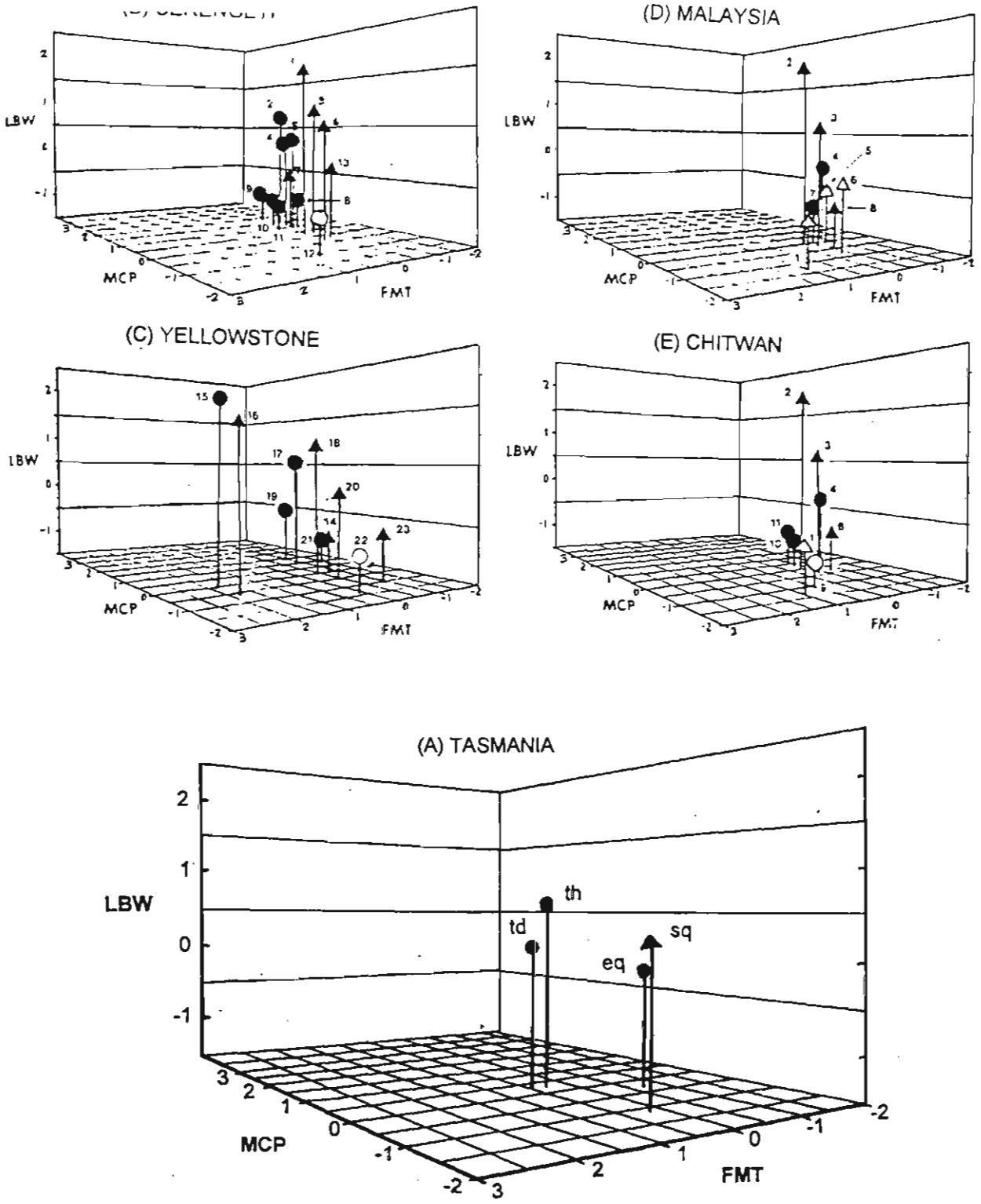


Figure 6.3 Locomotor morphospace and body size in mammalian carnivores. (A) Tasmanian marsupial carnivores, and placental carnivore guilds (B) Serengeti, (C) Yellowstone, (D) Malaysia, (E) Chitwan. (B - E) are copied from [Van Valkenburgh, 1985 #31].

Increasing values of metacarpal/phalanx ratio (MCP) correlate with a shift from closed habitat, ambush species to open habitat, pursuit species. Increasing values of femur/metatarsal ratio (FMT) represent slower moving species. LBW is log. body weight.

Locomotor classifications of species are as follows: Arboreal, open triangles; Scansorial, closed triangles; Terrestrial, dark circles; Semifossorial, open circles.

Species are as follows: (A) th, thylacine; td, devil; sq, spotted-tailed quoll; eq, eastern quoll (B and C) 1, lion; 2, spotted hyaena; 3, cheetah; 4, wild dog; 5, striped hyaena; 6, leopard; 7, serval; 8, golden jackal; 9, side-striped jackal; 10, black-backed jackal; 11, civet; 12, ratel; 13, caracal; 14, bobcat; 15, grizzly bear; 16, black bear; 17, wolf; 18, puma; 19, coyote; 20, wolverine; 21, red fox; 22, badger; 23, Canadian lynx (D and E) 1, binturong; 2, tiger; 3, leopard; 4, dhole; 5, Temminck's cat; 6, clouded leopard; 7, civet (*V. megaspila*); 8, fishing cat; 9, ratel; 10, golden jackal; 11, civet (*V. zibetha*). Placental carnivores (B - E) from (Van Valkenburgh, 1985).

6.4 Discussion

6.4.1 Significance of tooth wear and tooth breakage among marsupial carnivores

Teeth become worn as a consequence of processing (killing, biting and chewing) food. Tooth wear is progressive throughout an animal's life and may be used as an index of age in a variety of mammals, including both carnivores (Kruuk, 1972; Pemberton, 1990) and herbivores (Spinage & Jolly, 1974; Winter, 1980). Abrasiveness of the diet should determine the rate at which the teeth wear during the lifespan of an individual. In a sample of skulls from museum collections as used in this study which come from many sources, including deliberate collecting, roadkills, diseased animals and accidental deaths, individuals of all ages are represented. It is assumed that comparisons of tooth wear between species give a good indication of the comparative abrasiveness of the diet. Biases will exist if the samples are not of even age.

Among the marsupial carnivores, tooth wear is heaviest in devils. Devils consume all parts of a carcass, including the skin, even the two centimetre thick skin on the rump of a wombat, and all but the largest bones. This is a highly abrasive diet. Bones are gnawed and broken using the first two molar teeth, on which tooth wear is assessed in this study. Spotted-tailed quolls are intermediate between devils and the other species in the comparison, and are the only species where a sex difference is observed. Male spotted-tailed quolls have more tooth wear than females. This supports the dietary information on spotted-tailed quolls collected in this study (Chapter 3). Males consume large prey species, possums and macropods, and females are predators of small mammals, birds and insects. While spotted-tailed quolls do not consume bone, the skin of larger animals is tougher to penetrate, and could account for the greater degree of tooth wear in male spotted-tailed quolls than in females or smaller species of quolls. The thicker skin of large mammals is likely to be more abrasive for the small teeth of spotted-tailed quolls than for the relatively much larger and stronger teeth of devils. Thylacines, eastern quolls, western quolls and northern quolls have only a slight degree of wear on the teeth. This suggests a non-abrasive diet. The three smaller species of quolls - eastern, western and northern - are all predators of small prey, small mammals and birds, with invertebrates comprising a significant part of the diet. Such items are mostly soft and easy to process. It is of considerable interest, to note that this suggests that the thylacine had a non-abrasive diet. This means that the thylacine likely did not consume or gnaw bone and is unlikely to have consumed animals with very tough skin, such as wombats. In relation to its size, and the size of its teeth, the thylacine probably ate quite small prey.

Teeth of carnivores break because of unpredictable forces encountered during the killing of prey, usually involving contact with bone, or during consumption of very tough food such as bones (Van Valkenburgh, 1988*a*; Van Valkenburgh & Hertel, 1993). In a study of nine large placental carnivores and a herbivore, the zebra, Van Valkenburgh found evidence to support her suggestion that the diet of carnivores is an important determinant of tooth fracture frequency. Predators of large prey species

and consumers of bone have higher rates of tooth fracture than predators of small prey and invertebrates.

These ideas are supported by the incidence of tooth fracture in marsupial carnivores. Devils and spotted-tailed quolls have higher rates of tooth fracture than the smaller species of quolls. It is notable that the thylacine has a low rate of tooth fracture, equivalent to that of the small quoll species. In fact, there is even more evidence to support the contention of a diet of small prey species for thylacines. If the number and type of teeth that become fractured in each species is analysed by the number of each tooth type, thylacines are the only species in which tooth breakage is not different from expected. In other words, tooth breakage in thylacines is low in frequency and no tooth type, either incisors, canines, premolars or molars, are broken more often than would be expected by chance. This contrasts with quolls of all species, which break more canines than expected, and devils, which break more incisors and canines than expected.

The shape and function of canines predisposes them to higher fracture rates than other teeth. The long thin shape, necessary for stabbing prey in the killing process and for display in contests over food or mates, is more likely to break than the rounder and shorter shape of other teeth. Also the function of canines in killing, in tearing meat from a carcass and in fighting means that they are subject to more unpredictable bending stresses than other types of teeth. (Van Valkenburgh, 1988a) The high fracture rate of incisors as well as canines in devils can be explained by the killing method used with large prey. Devils bite any convenient part of the prey, shift their bite to the anterior end and hang on, often in a tug-of-war situation or being dragged along, until the prey succumbs (Chapters 2 and 5). The incisors would be subjected to more stress in this method of killing than in the more directed killing technique of the quolls where the canines are sunk into the back of the skull or neck with the prey dying from brain or spinal injury (Chapters 2 and 5).

Taking into account diet, killing method and tooth fracture in the devil and four species of quolls, it is suggested that the thylacine does not tackle prey items that are large relative to its body size. Thus, the canines of thylacines are not subject to large or unpredictable stresses during prey capture which may cause fracture. This is interesting in the light of work on canids which shows that they are only able to kill large prey if they hunt cooperatively (see 6.4.2, para 6 and 7).

6.4.2 Diet, locomotor and hunting modes of the thylacine

What was the ecological niche of the thylacine? The thylacine became extremely rare before the era of ecological field research in Tasmania, so almost nothing was recorded of its ecology and behaviour. What is known is reconstructed from bushmen's anecdotes and the behaviour of animals in captivity. Fortunately, much about its diet, locomotion and hunting mode can be inferred from comparisons of the morphology of skeletal remains, the teeth, skull and post-cranial skeleton with extant mammalian carnivores.

Superficially, the thylacine was the ecological equivalent of a large canid. It was a terrestrial carnivore with no adaptations for climbing. It had a long muzzle with well developed jaws like the canids. With a mean body weight of 25kg (range 15-30kg) (Smith, 1982) it was the same weight as the red wolf, *Canis rufus*, (15-30kg) and the African wild dog, *Lycaon pictus*, (20-27kg), and was intermediate in weight between the grey wolf, *Canis lupus*, (12-80kg) and the dingo, *Canis familiaris dingo*, (20kg), dhole, *Cuon alpinus*, (17kg) and coyote, *Canis latrans*, (11.5-15kg). All of these canids are pursuit or cursorial carnivores except the smallest, the coyote, which is primarily a pounce/pursuit predator of small mammals and only occasionally forms packs and hunts larger prey. (MacDonald, 1984)

What does morphological evidence tell us about the diet of the thylacine? Thylacines were carnivorous. Tooth microwear patterns are consistent with a carnivorous diet, and although its microwear patterns are different from the devil, which has a meat/bone diet, not enough is known yet of the effect of different diets on tooth microwear patterns to be able to further elucidate diet composition by this method (Robson & Young, 1990). Dental morphology of the thylacine, with extensive, longitudinal shearing crests (Archer, 1976), long relative blade lengths and small relative grinding areas indicate the thylacine had a carnivorous diet. However, the devil, which is known from this study (Chapter 3) to consume mostly large prey species such as pademelons, *Thylogale billardierii*, (4-7 kg), Bennett's wallabies, *Macropus rufogriseus rufogriseus* (11-15 kg) and wombats, *Vombatus ursinus tasmaniensis*, (26 kg) (Watts, 1994), prey that are the same size or larger than the devil (5-10 kg), has a dentition which is significantly more carnivorous than that of the thylacine. In fact, the thylacine lay between the devil and the spotted-tailed quoll, the largest and most carnivorous of the quolls, in the adaptations of its dentition to carnivory. This indicates that the thylacine probably regularly included smaller food items in its diet, food such as lizards, insects and even fruit, that required crushing and grinding rather than slicing as is appropriate for meat. In this respect, the thylacine is canid-like, rather than devil or hyaena-like. Canids differ from the more strictly carnivorous felids and hyaenids, in having a larger relative grinding area in their molar teeth. All canids, even wolves, which kill very large prey, are omnivorous to a degree, consuming large quantities of fruit and insects at some times of year.

There is further evidence in tooth wear and fracture rates, canine strength and skull shape that suggest that the thylacine probably mostly killed and ate prey smaller for its body size than did devils or the larger canids. Tooth wear on skulls from museums is very slight compared to the other dasyuroids and to the canids, indicating a lack of hard foods such as bones and tough skin, relative to its body size, in its diet (*Tables 6.9 and 6.2*). The degree of tooth wear for the thylacine was less than that for most of the canids, a group with omnivorous tendencies, and was comparable with the particular felid species that show the greatest amount of tooth wear. In general, the teeth of felids do not wear much because their diet is almost exclusively meat.

Table 6.9 Severity of wear on teeth of placental carnivores for comparison with marsupial carnivores in *Table 6.2*. Data derived from Van Valkenburgh (1988a)

Species		Percent in each stage of wear for all teeth		
	N	Slight	Moderate	Heavy
Felidae				
Panthera leo	121	67	24	9
P. onca	71	73	23	4
P. pardus	86	73	26	1
Acinonyx jubatus	46	87	9	4
Puma concolor	115	81	17	2
Hyaenidae				
Crocuta crocuta	77	29	60	12
Hyaena hyaena	57	40	42	18
Canidae				
Lycaon pictus	44	71	25	5
Canis lupus	112	46	40	13

The rate of tooth fracture in thylacines was very low, on par with the smaller species of quolls. Compared with all the other large dasyuroids, even the small species of quolls, the thylacine was the only species not to have a greater than expected tooth fracture rate for any tooth type. In all other species at least the canines break more frequently than expected for the number of teeth present. The devil and male spotted-tailed quolls have the highest rate of tooth fracture among the dasyuroids (*Table 6.3*). Both groups consume large prey species, that are also large relative to their body size (Chapter 3). Canines are used in killing, in tearing flesh from the carcass, as occlusal guides to direct the carnassial shearing function of the molars (Mellett, 1985) and in display and combat in contests over food or mates. They are subjected to more bending stresses than other tooth types and are the teeth most likely to fracture in large predators (Van Valkenburgh, 1988a). Thus in killing large prey in the case of male spotted-tailed quolls, and in consuming large prey including bones for devils, the canine teeth of these two groups are highly likely to contact bone and be broken. The low rate of tooth fracture suggests that the thylacine did not tackle large prey or prey where its canines were likely to contact bone during killing, the most likely way that canines are broken. Interestingly, the rate of tooth fracture is higher for most of the dasyuroids than for placental carnivores (compare with data in Van Valkenburgh (1988a). Thus tooth breakage rates for the thylacine were much greater than for the canids and even the hyaenids which have the highest tooth fracture rates of any of the placental carnivores. Van Valkenburgh & Hertel (1993) explained high fracture rates in now extinct Pleistocene carnivores at the La Brea tar pits in California as being the result of either low prey availability and more complete use of carcasses resulting in more contact of teeth with bone, or higher densities of predators resulting in intense competition over kills. She dismissed the idea of a local bias after comparison with a couple of other fossil sites in North America. The results from this study suggest that regional biases on the scale of different continents are important. This needs to be investigated further.

The thylacine appears to have had very gracile teeth. Its molar and premolar teeth were long, narrow and sharp. It had the narrowest premolars of any of the large dasyuroids, even the smallest, the northern quoll (*Figure 6.2*). This perception may be exaggerated however, by the extremely narrow snout of the thylacine. Even though it was much larger than the devil, the values for the thylacine for canine strength are weaker than those of the devil, although they are greater than those of the quolls (*Figure 2.3*, Chapter 2). However, compared to the canids, the canine teeth of the thylacine were intermediate between the maned wolf / African wild dog and the grey wolf in strength about the anteroposterior axis (Sx), which relates to killing behaviour, and were intermediate between the dhole / maned wolf and the wild dog / grey wolf in strength about the mediolateral axis (Sy), which relates to bite strength (*Table 6.10*). The dhole, wild dog and wolf are all pursuit carnivores that hunt in packs to kill large prey. The maned wolf is a pounce/pursuit carnivore, killing small vertebrates in much the same way as foxes do (MacDonald, 1984). So the thylacine was equivalent to the pursuit hunting canids in the canine strength index that relates to bite strength, but had weaker canines on the axis that relates to killing behaviour. Because it is in contact with bone which is likely to produce large oblique or mediolateral bending stresses during killing that tooth breakage is likely to occur, this indicates that thylacines were probably less likely to contact bone during killing than the canine, pursuit hunters of large prey, the wolf, wild dog and dhole. This suggests that thylacines killed prey small compared to their body size. An equivalent mediolateral strength relating to bite force, suggests that the prey size of thylacines may have included medium sized species.

Table 6.10 Values for canine tooth strength for marsupial and placental carnivores. Data for marsupials are from Chapter 2. Data for placentals are derived from Van Valkenburgh & Ruff (1987). Sx = canine tooth strength in bending about the anteroposterior axis; Sy = canine tooth strength in bending about the mediolateral axis

Species	Sx	Sy	Species	Sx	Sy
Dasyuridae			**Hyaenidae**		
Sarcophilus harrisii	3.13	3.56	*Hyaena hyaena*	4.61	6.52
Dasyurus maculatus	0.52	0.69	*H. brunnea*	8.34	11.75
D. viverrinus	0.22	0.33	*Crocuta crocuta*	6.18	8.69
Thylacinidae			**Felidae**		
Thylacinus cynocephalus	2.73	3.87	*Felis weidii*	0.78	1.03
Canidae			*F. yagourundi*	0.94	1.36
Vulpes velox	0.35	0.48	*Lynx rufus*	0.99	1.28
Lycaon pictus	2.52	3.93	*Felis caracal*	1.39	2.01
Canis lupus	3.01	5.61	*F aurata*	1.64	2.06
Urocyon cinereoargenteus	0.35	0.47	*F temmincki*	1.95	2.54
Vulpes vulpes	0.68	0.93	*F. serval*	1.54	1.99
Canis mesomelas	0.59	0.97	*F viverrina*	2.13	2.90
C. latrans	1.02	1.64	*Uncia uncia*	3.51	4.24
Dusicyon culpaeus	1.29	1.99	*Puma concolor*	4.76	5.88
Alopex lagopus	0.59	1.01	*Neofelis nebulosa*	3.19	4.13
Cerdocyon thous	0.56	0.94	*Panthera onca*	8.02	9.68
Nyctereutes procyonoides	0.55	0.84	*Acinonyx jubatus*	7.47	8.87
Otocyon megalotis	0.41	0.53	*Panthera pardus*	4.78	6.59
Speothos venaticus	1.54	2.13	*P. leo*	10.54	13.52
Chrysocyon brachyurus	2.28	3.57	*P. tigris*	15.42	21.53
Cuon alpinus	1.85	3.23			

Thylacines had a very long, narrow snout, most closely equivalent among the canids to that of a fox, second to that of a coyote and least of all to that of a wolf (Werdelin, 1986). A long snout means that the bite force at the canines is very weak. The canids as a group have the weakest bites of the Carnivora. They are only able to kill large prey by hunting in packs where enough bites can be delivered to the hindquarters of the prey to kill it (Radinsky, 1981a). When the limbs are adapted for cursorial locomotion as they are in the canids and in the thylacine, they are not adapted for food manipulation. This means the jaws must be used both for bringing down the prey and killing it (Ewer, 1973; Case, 1985). A weak bite means it is unlikely that the thylacine was able to kill prey large relative to its body size unless it hunted cooperatively.

Having established that thylacines were likely to have eaten prey fairly small compared to their body size, how did they hunt and kill it? Were they pursuit or pounce/pursuit hunters? In a comparison of limb and body proportions between thylacines and wolves, Keast (1982) confirmed Moeller's (1968) predictions that thylacines were overgrown dasyurids. Their body proportions do not differ from spotted-tailed quolls except that their front legs are longer and they stand straighter on their hind legs. They do not have the long legs of the specialised pursuit canid, the wolf. However, the body proportions of the thylacine are within the range of the generalised canids. The hindlimb/spine ratio of the thylacine (68%) - while less than that of the wolf (73%) - is within the range of the next smallest species, the coyote (69-71%), a pounce/pursuit hunter and the African hunting dog (65%), a pursuit hunter capable of matching the wolf in ranging ability, speed and stamina. The hunting dog has a hindlimb/spine ratio smaller than the coyote (Keast, 1982). However, it must be noted that the hunting dog lives in groups, cooperatively hunting mostly large prey over long distances like the wolf, while the coyote although sometimes cooperatively hunting large prey, catches predominantly small prey species which are hunted solitarily (MacDonald, 1984). The body proportions of the thylacine suggest that it was probably a pounce/pursuit predator capable of some prolonged pursuit (Keast, 1982).

Further support for this suggestion that the thylacine was probably a pounce/pursuit predator is provided in this study by the comparison of the femur/metatarsal ratio, another skeletal indicator of speed, of the thylacine with the placental carnivores (*Figure 6.3*) (Van Valkenburgh, 1985). On this ratio, the thylacine, along with the devil and the spotted-tailed quoll, is equivalent to some of the slowest of the placental carnivores, the semi-fossorial badger and ratel, the lion and the side-striped jackal (the bears are much slower again). There appears to be some phylogenetic constraint here on the limb proportions of the dasyuroids. Also, all of the larger dasyuroids (excluding the smaller quolls) have long metatarsals in relation to their femur length. Unlike in the placental carnivores, the granulated pad on the feet extends up the metacarpal and metatarsal regions as far as the wrist and heel joints. These extended pads lack the fleshy padding of the plantar surfaces. While all of the large dasyuroids are digitigrade when running, the extended pad area may be applied to the ground when the animal is walking slowly. Thus the large dasyuroids are not as well adapted for a digitigrade stance, which is necessary for cursorial movement, as are the placental carnivores. Also, on the metacarpal/phalanx

ratio, the thylacine was similar to pounce/pursuit and ambush predators that live in habitats intermediate between open and closed (*Figure 6.3*).

Synthesising all of the available morphological information, the diet and hunting mode of the thylacine appeared to be that of a carnivorous predator of mostly small to medium-sized prey species, small relative to its body size, that do not require prolonged or fast pursuit although it was probably capable of this at times. This hunting mode means it would most likely have been solitary. Most carnivores are solitary except where predator defence or hunting of large prey has selected for group-living (Sandell, 1989). While its body size was equivalent to a small wolf or canine pursuit predator of large prey, its body proportions, canine tooth strength, and likely prey size and foraging strategies were more akin to a coyote, a smaller pounce/pursuit predator of mostly small prey. There is no point searching for an exact ecological equivalent. Phylogenetic distance in several features of the morphology of the thylacine (skull shape (Werdelin, 1986) and foot pads) confirm that there are many variations on and combinations of morphology that produce what we classify as a dietary and hunting mode. Also, all of the larger canids, even grey wolves, eat substantial amounts of small prey, insects and fruit.

How do these conclusions based on morphometric analysis match with the anecdotal information available on diet and behaviour of the thylacine? From what has been gleaned from thylacine trappers and other bushmen, the thylacine appears to have been solitary, never hunting cooperatively and occupying a fixed home range (Guiler, 1985). No complete hunt has been recorded but reports of trappers are unanimous in stating that the thylacine was a slow but persistent runner, wearing its prey down over a long, steady chase until the prey collapsed with exhaustion (Guiler, 1985). This is consistent with reports from Sharland (1939) and LeSouef & Burrell (1926) reviewed in Smith (1982) which state that thylacines followed their prey for a long time at a trot, wear it down and finally rushing it. The similarly slow-moving devil has also been observed hunting in this fashion (Leon Barmuta, pers. comm., 1992; Peter, Joe's uncle, Marrawah, Tasmania, pers. comm., 1990). Prey species that have been mentioned are echidnas (Smith, 1982), pademelons and wallabies (Guiler, 1985). It is unclear whether wallaby refers to the smaller pademelon (4-7 kg) or the larger Bennett's wallaby (11-15 kg) because in the Tasmanian vernacular, the pademelon is called the rufous wallaby and the Bennett's wallaby, a kangaroo. No indication of the age or size of the individual prey items is given in any of the accounts. Information on habitat, which could give indications of foraging strategy, is highly suspect. Habitat is recorded as "hilly", "thick", "scrubby country" (Smith, 1982) but by the time these observations were made, the thylacine was already severely persecuted and had been removed from the more open habitats, which had become sheep farms. Also, before the arrival of the dingo, thylacines used to occur all over mainland Australia. Associations of herbivore species with marsupial carnivores in cave deposits strongly support the conclusions on prey size made in this study. Thylacines, which are thought to have used caves as lairs (Guiler, 1985) are most frequently associated with herbivores of small to medium body size, such as small species of *Macropus*, *Bettongia*, *Potorous*, *Trichosurus*, *Pseudocheirus* and *Isoodon* (Case, 1985). This is in contrast to *Thylacoleo*, which is associated most frequently with large prey species.

This synthesis has refined the description of the niche of the thylacine. In the past, authors have variously concluded that the thylacine was fox-like (Werdelin, 1986) or coyote-like (Moeller, 1968) based on its skull shape. Moeller (1968) found that, of all the placental carnivores, the body proportions of the thylacine were most similar to the clouded leopard, *Neofelis nebulosa*. In fact it is neither. It was a unique animal with some features of both the larger canine pursuit predators and some of the smaller pounce/pursuit predators.

6.4.3 Composition of the marsupial carnivore fauna of Australia; comparison of species diversity and ecological types with eutherian carnivore faunas on other continents

6.4.3.1 Ecological equivalence

The Australian marsupial carnivore fauna comprises a total of six species in the polyprotodont lineage, the Dasyuroidea. There are four species of *Dasyurus* (quolls), and one *Sarcophilus* (devil), in the Family Dasyuridae, and one *Thylacinus* (thylacine), in the Family Thylacinidae (Strahan, 1983). There are two further species of quolls in New Guinea (Flannery, 1990). These species are to a degree ecologically convergent with some of the major types and families of eutherian carnivores.

As described in the previous section, the thylacine was a large, terrestrial carnivore that was probably a pounce/pursuit predator of small to medium sized mammalian prey. In terms of ecological equivalence, it appears to have been most similar to the somewhat smaller canid, the coyote, although it was probably slower moving. Its longer jaw and tooth row length (Werdelin, 1986) means it probably had a weaker bite for its size than the coyote, but its larger body size for the same prey size range may have compensated for this.

A medium-sized pounce/pursuit carnivore of medium to large-sized mammals, the devil is a meat/bone specialist. While classified as terrestrial, it can and does regularly climb trees but is not particularly adept at this. It lacks special adaptations such as ridges on the foot pads but can rotate fore and hind paws in to hug the tree, in the manner seen in cats. The fleshy pad of the feet extends the full length of the carpal and tarsal bones, as in the thylacine, enabling a good grip for climbing. This is a feature in eutherian mammals seen only in arboreals (Taylor, 1989), but is a phylogenetic trait common to all dasyuroids. It is interesting that although the molar teeth are morphologically different from those of eutherian carnivores for reasons of phylogenetic history and the relative blade length measurement was not equivalent, the devil is in the same region of the three dimensional morphospace as the hyaenas (*Figure 6.2*). In fact the position of the devil on the axis for relative premolar size, an equivalent measurement representing the amount of bone in the diet, is more extreme than all of the hyaenas. So compared to all the other dasyuroids and the hyaenas, the teeth that are used for bone crushing in devils are very strong indeed. Devils consume all parts of a carcass except the very largest bones. The presence of white material in the scats that reacts with concentrated HCL (Hans Kruuk, pers. comm., 1991) suggests that they do digest some bone. Unlike hyaenas (Kruuk, 1972), however, devils do not digest all of the bone they consume. Each scat usually

contains several bone fragments, which may still be jagged and hence unaffected by digestion. Although devils do not possess the same degree of physiological adaptation to a scavenging role as the hyaenas, they are substantially more specialised for this role than the wolverine or the gray wolf - carnivores which show a tendency to bone consumption (Van Valkenburgh, 1989). Neither the wolverine nor the gray wolf have very robust bone-crushing teeth (*Figure 6.2*). Another morphological convergence with hyaenas is the position of the carnassial in the jaw (COM1). In most Carnivora, the carnassial is positioned at the point of maximum bite force (Werdelin, 1986). Radinsky (1981a; 1981b) found that the carnassial in hyaenids is closer to the condyle than in other carnivores. While this reduces the bite force at the carnassial, the bone-crushing premolar is brought further back in the jaw nearer to the point of maximum force. Considerable force is required to crush bones at this tooth, which is positioned relatively far forward in the weaker part of the jaw. While the position of COM1 in the dasyuroids is not directly equivalent to that in the Carnivora, relative to the other dasyuroids the main shearing crest (carnassial equivalent) in the devil is closer to the condyle (Werdelin, 1986). This is convergent with the bone consumption adaptations of the hyaena.

Spotted-tailed quolls are scansorial, small to medium-sized ambush predators of small to medium-sized vertebrate prey. Their diet is primarily meat. Observations of spotted-tailed quolls stalking and hunting (AnneMarie Watt, pers. comm., 1993) suggest they are ambush rather than pounce/pursuit predators. This species has the most pronounced sexual size dimorphism of all the large dasyuroids and this is reflected in their diet. Of the Tasmanian carnivore assemblage, the spotted-tailed quoll is alone in that the sexes consume significantly different sized prey (Chapter 3). Females take small prey species and males medium sized species. This prey size range, while it overlaps with small ground mammals and with large, terrestrial macropods, includes all of the arboreal mammal species, from pygmy possums to brushtail possums. While both the devil and the eastern quoll have some climbing ability, the spotted-tailed quoll is the only species with special adaptations for arboreality.

The three smaller species of quolls, the eastern, western and northern, are small terrestrial, pounce/pursuit predators of small mammals and birds, invertebrates and fruit. They fall into Van Valkenburgh's (1989) meat/nonvertebrate category. They replace each other geographically. The eastern and western quolls are similar in size. The northern quoll is smaller and is probably more insectivorous than the other two species. It also has climbing ridges on its foot pads and could be partly scansorial, but these are thought to be an adaptation to rocky habitats rather than climbing trees. (Strahan, 1983)

Van Valkenburgh (1989) only included large carnivores over seven kilograms in her analysis, so it is not possible to compare the quolls with equivalent-sized eutherian carnivores in three dimensional dental and locomotor morphospace. However, with relatively long jaws and tooth row length (Werdelin, 1986) and an unspecialised diet and hunting mode, the quolls as a group are most equivalent to the smaller viverrids. Their body proportions are also similar. The mustelids, by contrast, are highly specialised for hunting small mammals down burrows or tackling prey that are very large for their body size. They have a long, thin body with short legs

and short jaws like the felids which can deliver a very powerful bite for their body size (MacDonald, 1984; Werdelin, 1986).

There are three distinct morphological differences between the marsupial and eutherian carnivores which relate to phylogenetic distance and occur regardless of ecological convergence. These relate to skull dimensions, relative blade length and skeletal proportions. On skull dimensions, the large Dasyuroidea cluster as a group distinct from any of the Carnivora (Werdelin, 1986). Marsupial carnivores have a broad, flat skull with a very long rostrum. This could be partly because of the relatively small brain size of marsupial carnivores relative to eutherians (Nelson & Stephan, 1982; M. Jones, in prep.), which means that the height of the brain case and hence the occipital height are small relative to overall size. In turn, the skull, including occipital width and zygomatic arch width appears wide for overall size (Werdelin, 1986). An independent difference is the long rostrum. Canids, among the Carnivora, and secondly viverrids, have the longest snouts. Snout length influences bite strength at the canines, the longer the snout the weaker the bite, so it would appear that the dasyuroids have a very weak bite compared to their Carnivoran equivalents. This is probably not the case, however, because the small size of the brain in the Dasyuroidea means that there is a much larger space between the zygomatic arch and the brain case. The post-orbital constriction in dasyuroids is comparatively narrow. So the effect of a very long snout on bite strength is compensated by a much larger and presumably more powerful temporalis muscle. This is most evident in the devil, whose killing behaviour and bone-crushing habits mean that bite strength is paramount. Of all the dasyuroids, the devil has the shortest snout (Werdelin, 1986), strongest canines, the broadest zygomatic arch width and the smallest brain which provides maximum volume for the temporalis muscle.

The Dasyuroidea appear to have a long relative blade length compared to equivalent Carnivora (*Figure 6.2*). There is difficulty, however, in defining which shearing blades in the dasyuroids are equivalent to the carnassial in the Carnivora. Unlike eutherian carnivores, dasyuroids have little regional differentiation of the teeth, although there is some. Each molar has a shearing and a crushing part. The length and height of the shearing blade increases towards the rear of the mouth, corresponding with a decrease in the relative grinding (crushing) area of the tooth (Archer, 1976). The first two molars become quite worn during the individual's life decreasing their usefulness as a cutting blade (most in devils, least in thylacines) while the posterior two molars remain sharp. Werdelin (1986) measured COM_1, the length from the condyle to the carnassial notch in Carnivora (Radinsky, 1981a), in what he felt was the equivalent position in dasyuroids, the notch between the paraconid and protoconid of M_5, the posterior most lower molar. Werdelin concluded that the last molar was the equivalent tooth to the carnassial but that the position of COM_1 in dasyuroids was slightly closer to the condyle than in eutherians. I dissent from this conclusion. Because the second last molar also remains sharp throughout the life of the animal, it is possible to conclude that the shearing function is shared between the last two molars. The exact role played by each tooth will require a detailed study of jaw mechanics and occlusal mechanisms. It is interesting to note that the crushing function in marsupials seems to be carried out further forward in the jaw, where bite strength is weaker, than in eutherians. The first two molar teeth have the largest crushing areas in dasyuroids. In the Carnivora, it is the

post-carnassial molars at the back of the mouth where bite strength is relatively great that carry out this function.

The third main phylogenetically related difference is that all marsupial carnivores, compared by the femur/metatarsal ratio, appear to be slower runners than eutherian carnivores (*Figure 6.3*). The thylacine, the devil and the spotted-tailed quoll, on directly equivalent measurements, lie in the same part of the morphospace as the slow moving, semi-fossorial badger and ratel. So, even though none of the marsupial carnivores are fast pursuit carnivores, they appear to be slower moving than all of their eutherian pounce/pursuit or ambush counterparts.

6.4.3.2 Composition of carnivore assemblages

What are the differences in the composition of the carnivorous marsupial fauna of Australia compared with assemblages of eutherian carnivores on other continents? The Australian lineages of marsupials evolved in isolation from all other continents from when the Australian plate split from Antarctica and Gondwanaland in the middle Eocene, 45 mya, until the decreasing distance between Australia and Asia enabled eutherian vertebrates to raft or walk (over land bridges during glacial periods) across from the Indonesian Archipelago, a period that began in the Miocene, about 15 mya (Heatwole, 1987). By contrast, there have been greater opportunities for faunal interchange between all other continents, with substantial land bridges of long duration with adjacent continents. The marsupial carnivore fauna of Australia has been isolated from eutherian carnivores until very recently, somewhere between three and a half thousand and perhaps as long as eight thousand years ago when the dingo, the first eutherian carnivore to join the Australian fauna, arrived (Archer, 1981).

There has been a total of six species of large marsupial carnivores in Australia in recent times. Local faunas are smaller. When European peoples first colonised Australia, the following local distributions of carnivore assemblages existed. In Tasmania, there were four species, the thylacine, the devil, the spotted-tailed quoll and the eastern quoll. In the wetter southeast part of the mainland, from the south-east of South Australia through Victoria and eastern NSW to south-east Queensland, there were only two species, the spotted-tailed and eastern quoll. In the wet north-east part of Queensland, two species of quolls, the smaller northern sub-species of the spotted-tailed quoll, and the northern quoll coexisted. Elsewhere in Australia, with perhaps the exception of the deserts, one species of quoll comprised the total marsupial carnivore fauna. The range of the northern quoll did and still does extend across the wet-dry tropics, the northern most latitudes, from west coast of Western Australia to the east coast of Queensland and southwards through the fairly dry parts of the east coast as far as south-east Queensland. The western quoll was distributed over much of the arid zone of Australia and the wet south-west of Western Australia, perhaps overlapping with the other three quoll species at the edges of its range. Its past distribution is not well documented. The eastern, western and spotted-tailed quolls have declined in distribution and abundance this century as a result of habitat destruction and the impact of eutherian carnivores introduced by European peoples. This study is based on recent, pre-European distributions. (Strahan, 1983)

The thylacine persisted on the mainland of Australia until 3280±90 years b.p. in south-west Western Australia (Partridge, 1967) and possibly until European times (0 ±80 yrs b.p.) in the Kimberley region of north-west Western Australia although this record is contentious (Case, 1985). Devils existed on mainland Australia until 3120± 100 yrs b.p. in the Northern Territory and 430±160 yrs b.p. in south-west Western Australia (Archer, 1981). The fossil record is too poor to draw late Quaternary distribution maps but the available evidence suggests that neither the thylacine nor the devil were adapted to arid environments. There are records of the thylacine from central Australia in the Miocene when this region was warm and wet, and records of thylacines in New Guinea but the only recent records of thylacines and devils are in currently more mesic parts of Australia. (Keast, 1981)

The major differences between the large-bodied marsupial carnivore fauna of Australia and eutherian carnivore assemblages on other continents, at both a local and a continental scale, are the lack of some major morphological/hunting types that are represented in the Carnivora and the paucity of species.

Comparing the extant Australian marsupial carnivore fauna with eutherian carnivores *Figure 6.2* and Werdelin (1986), reveal that Australia lacks both a felid or mustelid -like meat specialist, that has short powerful jaws and dentition highly adapted for carnivory, and a nonvertebrate/meat omnivore such as the bears. There has been a felid-like carnivore in the Australian fauna in the past, however. Evidence from wear striae on molar teeth strongly suggest that *Thylacoleo*, a leopard-sized and at least partly arboreal diprotodont marsupial, was carnivorous (Wells, Horton & Rogers, 1982). This conclusion has recently been supported by the demonstrated use of diprotodont-like incisors as stabbing weapons by the South American caenolestids, and by the recent discovery of fossil kangaroo bones bearing alleged thylacoleonid tooth marks (Clemens, Richardson & Baverstock, 1989). The third premolar was modified into a long shearing crest which functioned as a carnassial and the diprotodont incisors are thought to have been used to kill the prey by a slash to the throat or suffocation in the same way that felids kill prey larger than themselves. Powerful, clawed forearms, also found in sabretooth cats, would have compensated for the lack of interlocking canines in pulling down and manipulating the prey for the kill (Finch, 1982; Case, 1985). *Thylacoleo* is thought to have killed large prey species. While the thylacine is consistently found in cave deposits with small to medium-sized herbivores, *Thylacoleo* is consistently found associated with large to very large herbivores, four of the six taxa found most frequently associated with *Thylacoleo* remains, *Sthenurus*, *Diptotodon*, *Protemnodon* and *Macropus titan*, are members of the Pleistocene megafauna (Case, 1985). A leopard-like niche has been suggested for *Thylacoleo* (Wells, Horton & Rogers, 1982). The phylogenetic relationships of *Thylacoleo* are still being debated but it is thought to be more closely related to the Vombatoidea, koalas and wombats than to the Phalangeroidea, the possums. Given the proclivity for eating meat among the brushtail possums, it is possible to see how a carnivorous species could have evolved from this normally herbivorous group (Archer, 1981). *Thylacoleo* survived well into the Pleistocene and may have overlapped with the first aboriginal people in Australia.

There does not appear to have been any large, omnivorous, bear-like dasyuroids or other marsupials in the Australian fossil record. Bears are also lacking in the

extant African fauna, although extinct species are found in the fossil record (Van Valkenburgh, 1989). Bears exist in the North American fauna because of their ability to hibernate when seasonal food becomes scarce (Van Valkenburgh, 1989). Smaller omnivores such as brushtail possums partially fill this role in Australia but there are no large species in the marsupial fauna able to use winter torpor as a mechanism for surviving food shortages (Fritz Geiser, pers. comm., 1993). Archer suggests, on the basis of dental morphology and wear striae on the premolars, that the extinct giant rat kangaroos, *Propleopus*, which existed up until the Pleistocene, may have been carnivorous or at least omnivorous. There is current evidence that the herbivorous diprotodont marsupials can evolve into omnivorous species which eat meat. Brushtail possums, *Trichosurus vulpecula*, (this study) and the potoroid, *Bettongia leseur*, are known to scavenge from carcasses and the smallest potoroid, *Hypsiprymnodon moschatus*, is omnivorous. (Archer & Flannery, 1985)

Australia has a very low species diversity of marsupial carnivores, with only six species and between one and four species in local faunas. By Van Valkenburgh's (1985; 1989) definition of large carnivores, those over seven kilograms, there are only two in Australia, the thylacine and the devil, both recent members of the Tasmanian fauna. This is compared to ten species of large mammalian carnivores in Yellowstone, eight in a Malaysian local fauna and thirteen in the Serengeti.

What might the reasons for the paucity of species be? The primary reason is probably poor soil nutrients. Aridity and evolutionary stochasticity may also play a role. Australia is unique among the continents of the world in that most of the rocks and soils are very ancient. With the exception of the Eastern Highlands, the continent of Australia has not been disturbed by episodes of mountain building or active volcanoes for three hundred million years. These processes have, on other continents, reduced the extent of very ancient rocks and soils to small areas (Frakes, McGowran & Bowler, 1987). Millions of years of weathering and leaching have produced soils that are among the most nutrient poor in the world, particularly in phosphorus, nitrogen and potassium (Bridgewater, 1987). Sclerophylly, expressed in the Australian flora more widely than on any other continent, is a response to nutrient poor soils (Barlow, 1981; Specht, 1981a). The effect of poor soil nutrients impacts through all trophic levels of the ecosystem (Westoby, 1988). Van Valkenburgh (1989) found evidence to support her predictions that environments with a higher diversity and abundance of herbivore prey species also had a higher species diversity of carnivores. There is good evidence in eucalypt forests in Australia that the diversity and density of arboreal marsupials correlates with levels of nitrogen, phosphorus and potassium in the foliage and soils (Braithwaite, Dudzinski & Turner, 1983; Braithwaite, Turner & Kelly, 1984), and bird species richness correlates with magnesium, a trace element important in forest productivity (Braithwaite *et al.*, 1989). Distribution and density of arboreal browsing marsupials is directly limited by soil fertility. Anti-browsing toxins present in eucalypt leaves, such as phenols, reduce digestive efficiency and the utilisation of available nitrogen for browsing marsupials. These toxins are in higher concentrations on poor soils (Cork & Foley, 1995). Sclerophylly and evergreeness may also shape other aspects of assemblages, such as the breeding biology of insectivorous birds in eucalypt forests (Woinarski, 1985). In the absence of data on biomass of prey species for comparison with Van Valkenburgh's (1989) study, it seems fair to say that the very old, low nutrient soils

in Australia may have prevented both the evolution of very diverse local prey faunas and the development of very dense concentrations of herbivores as are found in the Serengeti.

What is the effect of aridity? Structural complexity of habitat provides opportunity for different modes of locomotion and hence escape strategies of prey and different hunting modes of predators. Low structural complexity of habitat correlates with a low carnivore species diversity (Van Valkenburgh, 1985). Increasing aridity in Australia since the Middle Miocene has caused a reduction in structurally complex, closed forests and an expansion of sclerophyllous woodlands, shrublands, spinifex (*Triodia sp.*) and grasslands (Specht, 1981b). Perhaps the spread of structurally less complex vegetation is partly responsible for the low species diversity of carnivores in Australia. This argument of the effect of aridity does not seem to hold for the Australian environment. It implies that there would have been higher species diversity in the Miocene when wet, closed forests covered much of Australia. This was not the case. The marsupial fauna of Australia divides into two groups, the mesic-adapted fauna whose lineages can be traced back to the Miocene which retreated to the cool, wet Eastern Highlands, and a more recent radiation of arid-adapted species which are not closely similar to Miocene forms (Archer, 1981; Clemens, Richardson & Baverstock, 1989). As there is still habitat available for this mesic fauna and many species persisted to recent times, the effect of increasing aridity could also have been to increase species diversity of carnivores since the Miocene as arid-adapted species evolved. This is also not the case. Species diversity of mammals in Australia and also of marsupial carnivores is highest in the wetter, forested areas and lowest in the deserts (Pianka & Schall, 1981).

The paucity of large (>7 kg) carnivores in the Australian fauna today is probably related to the low species diversity of large herbivores. The only really large species of extant herbivores are the red (*Macropus rufus*) and grey kangaroos (*M. giganteus, M fuliginosus*), wallaroos (*M. robustus, M. antilopinus, M. bernardus*) and wombats (25-60 kg), at least the young of which could be killed by devils. Large body size in herbivores, a world-wide phenomenon during the Tertiary, is thought to have evolved in response to the spread of coarse, low nutrient vegetation with increasing aridity. Larger animals need less energy per unit body weight to sustain themselves so can exist on bulkier forage of lower nutritional value, and can better tide over periods of food shortage than smaller herbivores. The herbivorous, megafaunal species which evolved in Australia, essentially giant kangaroos, wombats and diprotodons, were unable to survive the increasingly long, arid periods of the Pleistocene. Inability to survive water shortage, and slow reproductive rate and therefore recolonising ability are thought to have contributed to their extinction (Main, 1987). Along with them, the only predator of large prey species, *Thylacoleo carnifex*, also became extinct. *Thylacoleo* disappeared about the time that aboriginal people, also large carnivores, arrived. There is some suggestion, but no evidence, that aboriginals may have contributed to the extinction of the megafauna, including *Thylacoleo*, but the explanation of increasing aridity is more compelling. Remember also that fossil distributional evidence suggests that the thylacine and the devil were not arid-adapted and before they disappeared from the mainland were probably restricted to the wetter southeast and southwest of the continent.

A possible explanation for the paucity of large carnivore species in the Australian marsupial fauna is extinction without replacement, as has been shown for the Yellowstone carnivores (Van Valkenburgh, 1989). The fossil record indicates that this is an unlikely explanation in Australia. Although six species of thylacoleonids have been recorded, in only one fauna or fossil deposit, the Pliocene Bow Local Fauna, have two species of *Thylacoleo* been recorded as existing sympatrically (Archer, 1981; Archer & Dawson, 1982; Archer & Rich, 1982). Up to five other species of thylacine besides *T. cynocephalus* are known so far from the fossil record, but none of these is known to be contemporaneous with any other species of thylacine (Archer, 1981; 1982; 1984; Dawson, 1982b). At least two other species of devils are known from the fossil record, *Sarcophilus laniarus*, a larger version of *S. harrisii* from the Pleistocene and a small Plio-Pleistocene devil. *Glaucodon ballarentsis*, a carnivore that shared features of both spotted-tailed quolls and devils existed during the Pliocene and at least one other species of quoll, *Dasyurus dunmalli*, has been recorded (Archer, 1981; Crabb, 1982; Dawson, 1982a). There is no evidence that the marsupial carnivore fauna was richer at any time in the past than today. New work on fossil assemblages may reveal this.

The extensive radiation of varanid lizards in Australia has been put forward as part of the reason for the low species diversity of marsupial carnivores. (Pianka, 1969; 1994; Hecht, 1975; Rich, 1983). The diet and habitat of living varanids overlap with those of the quolls. There are terrestrial and arboreal species, which consume a variety of invertebrate and small to medium sized vertebrate prey (Greer, 1989). In the Pleistocene, *Megalania prisca*, a varanid twice the size of the living komodo dragon, was the largest terrestrial predator in Australia. Given that komodo dragons are capable of bringing down a bullock by hamstringing it, *Megalania prisca* may have been able to kill a diprotodont (Rich, 1983). The only other carnivore in Australia at that time which may have been capable of killing large prey was *Thylacoleo*. The Australian radiation of the Varanidae is more diverse than anywhere else in the world, comprising 24 of the 36 known species. The remainder are in south and south-east Asia and Africa (Greer, 1989). Pianka (1994) asks if adaptive radiations of varanids were precluded from these regions by the presence of a fairly diverse fauna of small foxes and viverrids and I would add a diverse fauna of large mammalian carnivores. Conversely, several authors have suggested that varanids arrived in Australia at a time when the dasyuroids had not yet expanded to fill the available niches (Storr, 1964; Pianka, 1969; Hecht, 1975). This is the idea of "empty niches" which probably never exist. Also, this last idea falls down when the time scale of the respective radiations is considered. Varanids are thought to be a late Tertiary (middle Miocene) arrival in Australia from Eurasia (Pianka, 1994). At this time, the marsupial carnivore fauna of Australia was already well established.

There are some correlations, however, which are worthy of further consideration. Lizard diversity in Australia, including that of the varanids, is highest in dry, sunny arid regions, whereas the diversity of all other vertebrate fauna, including marsupial carnivores increases with rainfall (Pianka & Schall, 1981). Before the arrival of eutherian carnivores in Australia, upon which distributions of some species radically changed, all but two of the six species of large dasyuroids (western and northern quolls) appear to have been restricted to the wetter regions. There are fewer species of varanids in these regions than in the drier parts of Australia (Cogger, 1992). Few

inter-continental faunal comparisons have been carried out but they show that continents are similar to each other except for Australia which is unique in some respects (Heatwole, 1987). Australian deserts, have a very high diversity of lizards (Pianka, 1969; 1973) and low diversity of mammals (Morton, 1979) compared with deserts in North America and Africa. Ecological roles played by mammalian carnivores and granivores in North America are filled by varanids and granivorous birds and ants in Australian deserts. Australian deserts differ from those elsewhere by experiencing periods of heavy rains followed by long droughts, conditions which mammalian granivores are not easily able to adapt to physiologically (Morton & Baynes, 1985). The physiological options provided by the heterothermic existence of reptiles mean they are better able to adapt to these conditions. While Australian deserts lack the high densities of granivorous rodents, there is an extensive radiation of insectivorous marsupials - very small dasyurids - although they are not in high abundance. The total number of insectivores, both lizard and mammal, is in fact much higher in Australian deserts perhaps because of the large number of ants and termites (Heatwole, 1987). The paucity of small mammal species as prey for marsupial carnivores and the high abundance and diversity of lizards is said to have led to the varanid lizards being the dominant predators in Australian deserts. It appears as though, at least in the more arid parts of Australia which is two-thirds of the continent, that lizards in general and varanids in particular, have been more successful. Twenty two percent of Australia is covered by hummock grassland dominated by *Triodia sp.*, plants with a persistent sclerophylly, to the extent that the leaves do not die and form a litter layer. Nutrients in this system are recycled either through herbivory of green leaves or by termites, which consume the dry leaves. Reptiles can easily adapt to exploiting termites, especially the legless and reduced limb lizards that are abundant in the Australian fauna, and the hummocks provide a complex habitat. Both the extensive areas of hummock grassland supporting large numbers of termites and the complexity of this habitat are thought to contribute to the very high species diversity of lizards in arid Australia. (Morton & James, 1988)

The question to ask may be what the environmental factors are which influence the distribution and density of varanids and marsupial carnivores in both arid and mesic parts of Australia? The preceding information suggests that extreme sclerophylly related to poor soil nutrients favours termites which favours the radiation of a lizard fauna. This is coupled with heavy rain / long drought cycles, conditions which mammals find difficult to cope with physiologically, but which again favour the evolution of an extensive reptile fauna. For the same reasons, mammalian carnivores, but not reptilian carnivores, would not easily adapt to this environment. This is the strongest argument. The argument that reptilian predators have evolved to exploit the rich lizard fauna does not really hold. There is no reason why mammalian carnivores can not consume reptile prey or reptilian carnivores mammalian prey. There is also the possibility that the high diversity and densities of lizards in Australian deserts and the low diversity of mammals, compared to the situations that have evolved on other continents, may be no more than a stochastic outcome of evolutionary history.

6.5 Conclusions

The major differences between the marsupial carnivore fauna of Australia and eutherian carnivore faunas on other continents are the paucity of species in the Australian fauna and the restricted number of the main eco-morphological types that occur among the eutherian carnivores. The marsupial carnivore fauna of Australia evolved in isolation for a very long period of its evolutionary history. It is, therefore, an ideal natural experiment to examine the relative influences of evolutionary history and physical environmental factors.

In summary, the most likely explanations for the low diversity of species and eco-morphological types of marsupial carnivores in the Australian fauna are poor soils, aridity and evolutionary stochasticity. The ancient and low nutrient status of the landscape and soils results in a low biomass and density of prey species and hence of carnivore species. Widespread aridity may also play a role in limiting the diversity and size of the herbivorous megafauna and hence the large carnivores. The answer may well be a combination of available genetic stock (ie. varanid lizards), soil nutrients and aridity. The explanation may also be just evolutionary stochasticity.

These conclusions are in agreement with Westoby's (1988) survey of studies of intercontinental comparisons which concluded that virtually all ecosystem characteristics are strongly influenced by the present day environment. The influence of evolutionary history is not as evident. This is also the case in the marsupial carnivore fauna of Australia, which have evolved in isolation to the eutherian carnivores. Not only has carnivory evolved independently, but ecological convergence to the main morphological / dietary / hunting types has also occurred. Advances in the understanding of why species diversity of particular taxa vary from continent to continent requires rigorous comparisons of the environmental factors that determine species richness for the taxa in question.

Chapter 7 General Conclusions

Evidence that competition has been and probably still is a significant structuring force in the guild of large marsupial carnivores in Tasmania was found. Evolutionary evidence, indicative of competition as a significant factor influencing morphological size relationships among species in the guild in the past (the "ghost of competition past" as Connell (1980) put it), is present as character displacement and morphological patterning among the quolls in Tasmania. This patterning is expressed in the form of equal size ratios of canine strength between adjacent morphospecies of eastern and spotted-tailed quolls in Tasmania. That the patterning occurs in canine strength is consistent with the feeding ecology of these species of marsupial carnivores and, therefore, with the hypothesis that competition for food resources is the underlying factor. Character release occurs in the guild of marsupial carnivores, comprising the same quoll species as in Tasmania, on the adjacent southeastern part of the mainland of Australia. The two larger Tasmanian species, the devil and the thylacine, have been absent from this region for a long time, suggesting that it is the extra pressure on the food resource from these two species in Tasmania that is intensifying competition among the two more similar, congeneric quolls, resulting in character displacement.

The existence of current competition in the Tasmanian marsupial carnivore guild at Cradle Mountain can be inferred from this study. A greater extent of dietary overlap between spotted-tailed quolls and adjacent species when guild members are ranked by size, than is experienced by either eastern quolls or devils, correlating with the relative rarity of spotted-tailed quolls suggests that competition is still an active structuring force in the guild. Within the limitations of an observational study, however, inferences only can be made that spotted-tailed quolls are likely to experience more competition than do the other two species. Active depressive competition can result in reduced populations (Begon, Harper & Townsend, 1990). This may explain why spotted-tailed quolls are rare compared to the other two species.

It is of interest that while competition, as inferred by niche overlap, involves all extant members of the guild, morphological patterning is evident only among the morphospecies of quolls. This implies that competition is most intense between the two most similar species in the guild, the congeneric quolls. This is consistent with generalisations made from many studies that while competition may be an important force in a community, it is likely to affect only species interactions at the lowest levels of organisation, that of the guild (Begon, Harper & Townsend, 1990). In this case, competition within the guild is most evident between the most similar species. This demonstrates some of the fuzziness with the guild definition (Simberloff & Dayan, 1991). Although the definition of a guild as used in this study is ecological (species that use the same class of resources in a similar way), similar species are usually also closely related taxonomically (MacNally, 1983). The more taxonomically closely related species are , the more similar they are likely to be. For

instance, it could be argued that the two quoll species comprise a guild on their own. excluding the devil and the thylacine, on the basis of similarity in killing behaviour (a crushing bite applied to the back of the skull or the neck). Killing behaviour at least of the devil, involving a tenacious, crushing bite to the most convenient part, usually at the anterior end, is different. That of the thylacine is unknown. I have included all four species in the same guild on the basis of a generally similar killing behaviour. All of the large dasyuroids employ an unspecialised killing bite that is designed to crush the prey, usually at the anterior end. The differences in prey killing technique between the quolls, the devil and the thylacine may be partly an allometric effect, relating to the size and strength of prey. A more likely explanation is that the differences relate to other aspects of feeding ecology. In tooth dimensions, skull shape and body proportions, the thylacine is more similar to a scaled up quoll. It is the devil, with a short, broad robust skull, teeth and body which is the odd species. These features relate to the scavenging adaptations of the devil which are lacking in the other two species.

Competition operates by exploitation and depletion of resources or by direct interference between individuals which restricts access to a resource. Resource partitioning, or differential use of resources, functions to decrease niche overlap and therefore potentially decreases both exploitation and interference competition between species. In the Tasmanian guild of marsupial carnivores at Cradle Mountain, resource partitioning is occurring on at least three niche dimensions, diet, vegetation type and vertical use of the habitat. Where overlap between species is high on one dimension such as food, another niche dimension is partitioned, as predicted by (Schoener, 1986). This may be important in reducing competition between female spotted-tailed quolls and eastern quolls. Although diet overlaps significantly, they forage in completely different habitats with little overlap. Partitioning of the habitat on a vertical scale requires specialised morphological adaptations, just as partitioning on prey size requires the evolution of different sized trophic structures, and represents niche partitioning on an evolutionary time scale.

Interference competition among the marsupial carnivores at Cradle Mountain is most likely to occur over carcasses of large prey species. While all three species scavenge, the devil is the primary scavenger, exhibiting morphological, physiological and behavioural adaptations that are lacking in the two quoll species. Interspecific dominance is influenced mostly by body size, but age can also be significant. In most situations devils dominate carcasses. Devils are also by far the most abundant of the three carnivore species at Cradle Mountain and in Tasmania overall. Highest abundance and greatest contribution to the energy flow in the local ecosystem by the largest species in a local assemblage has been reported across a wide spectrum of animals and plants (Brown & Maurer, 1986). Brown suggested this was because of the physiological advantages of large body size and greater mobility, but also that larger species can competitively dominate resource use. The numerical dominance of the Tasmanian marsupial carnivore guild by devils may relate to their competitive dominance in interspecific contests over food.

Intraspecific competition has not been considered throughout most of this study and needs to be addressed, especially in devils. Dietary overlap and interference competition over carcasses indicate that intraspecific competition could be strong for

devils. Significant differences in diet between the sexes and nearly 100% sexual size dimorphism in body weight indicate that, among the three species, intraspecific competition is probably least important for spotted-tailed quolls.

Aspects of guild structure, such as size relationships, morphological adaptations for utilising prey and relative abundance of carnivore species, are influenced by several underlying factors, of which competition is important. Guild structure of the large marsupial carnivores in Tasmania and the causal factors underlying it can be summarised as follows.

The three species of carnivores have evolved at different sizes. Prey are partitioned by size and body size of carnivores is correlated with prey size. The fractal dimensions of the habitat which shapes the body size of all the mammal species at Cradle Mountain has resulted in a size distribution of the prey species consisting of two size-clumps. This has, in turn, influenced the body size of the carnivores. The carnivores divide into two groups based on prey size which relate directly to the size-clumping of prey species; devils and male spotted-tailed quolls which consume mostly larger prey species, and female spotted-tailed quolls and eastern quolls which consume mostly smaller prey species. Within these groups there are significant overlaps in diet. The prey size range of the middle-sized carnivore , the spotted-tailed quoll, covers both the large and the small size-clumps of prey. As a result of this, sexual size dimorphism in body size, including body mass and canine strength, is greater in spotted-tailed quolls than in either devils or eastern quolls. This occurs both in Tasmania and on the mainland where the devil is extinct. Latitudinal size correlations influence the overall size of eastern quolls, with those in Tasmania larger than those on the mainland. The same size gradient is expected to occur among spotted-tailed quolls, but in fact, females are the same size in Tasmania as they are on the mainland and males, while they are the same body size in both regions, have smaller values for canine strength in Tasmania than on the mainland. What seems to be happening in Tasmania is that the presence (until very recently) of two larger species of carnivores has added an extra pressure on prey resources, resulting in competitive character displacement in the two most similar species, the congeneric quolls. Character displacement has operated on canine strength, the trophic structure most closely related to foraging or killing behaviour, resulting in equal size ratios between adjacent morphospecies. The effects of this have been to reduce canine strength in the spotted-tailed quolls in Tasmania, and reduce the degree of sexual size dimorphism in canine strength in both species of quolls in Tasmania compared to the mainland, although the reduction has been greater in spotted-tailed quolls. This presumably has reduced competition between the two species. The prey size/body size correlation and weak patterning of prey size (weak because the patterning is disrupted by the clumping in the size distribution of the prey) support the hypothesis of competitive character displacement. Sex differences in canine strength, probably resulting from sexual selection, are also evident in the quolls, but it is not known how this affects the observed morphological size relationships.

Size relationships of canine strength and body weight among the morphospecies of marsupial carnivores both in Tasmania and on the mainland, therefore, result from a complex interaction of latitudinally correlated size variation, competitive character

displacement, size distributions of prey species which relate to the hierarchical geometric scale or fractal dimensions of the habitat and sexual selection.

Locomotor morphology, habitat use and foraging strategy of the carnivore species are shaped by the activity substrate or behavioural and morphological dimensions of habitat use of the prey species. Prey size is correlated with body size of carnivore. A high proportion of the diet of the medium-sized carnivore, the spotted-tailed quoll, consists of medium-sized prey. In Tasmania, most of the medium-sized prey are arboreal and most arboreal species are medium-sized. The spotted-tailed quoll, therefore, has morphological adaptations for climbing which are lacking in the smaller and the larger species, the eastern quoll and the devil, respectively. Most of the small and the large prey species are terrestrial.

One of the effects of competition is to depress populations of one or more species. The species comprising the guild of marsupial carnivores at Cradle Mountain have widely disparate relative abundances. It can be inferred from this study that extent of dietary overlap and subsequent competition (which would only occur if resources became limiting) may explain the scarcity of spotted-tailed quolls. The high abundance of devils may be due in part to their competitive dominance in feeding situations. To test these tentative assertions would require manipulative experiments. Eastern quolls reach much higher densities in areas of extensive sub-alpine grasslands near the Cradle Mountain study site (Dianne Moyle, pers. comm., 1994). As eastern quolls exhibit a strongly significant difference from both devils and spotted-tailed quolls in preferred vegetation or habitat type, the abundance of eastern quolls at Cradle Mountain may be nothing more than a reflection of the amount of suitable habitat available. Cradle Mountain consists of a mosaic of rainforest, eucalypt forest, buttongrass moorland and relatively small areas of grassland. Eastern quolls reach their highest densities in grasslands in Tasmania.

The results from this study are in agreement with Westoby's (1988) observation that ecosystem characteristics are more strongly influenced by the environment than by evolutionary history. Although the terrestrial vertebrate fauna of Australia has been isolated from that of other continents for most of its evolutionary history, carnivory has evolved independently in the marsupials and ecological convergence with the eutherian carnivores has occurred. The major difference in composition between the Australian marsupial carnivore fauna and the eutherian carnivore fauna of other continents is the low diversity of both numbers of species and of eco-morphological types. This is the case in the extant fauna of Australia and is to a slightly lesser extent present in the fossil faunas. The most likely explanations for this are the poor soils and aridity of the Australian continent.

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